THE CONTEMPORARY SCIENCE SERIES

THE NATURAL HISTORY OF DIGESTION

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ILLUSTRATED BY FIGURES, DIAGRAMS, AND CHARTS

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PREFACE.

Civilised man habitually ill-treats his digestive organs. One who would never venture out on a chilly day without some extra covering to protect his lungs, seldom has any such regard for his stomach, nor hesitates irregularly and irrationally to introduce into this long-suffering organ all manner of articles fancied by his senses. The possession by man of a cultivated palate, of highly though delicately trained senses of taste and smell, and of an appetite peculiar to his species, which can be habituated to all kinds of unusual flavours and *bizarre* tastes,—in many instances with the development of a craving for them,—is not an unmixed blessing. Stimulation of the appetite with highly-flavoured foods diminishes the natural wish for food for its own sake, it tends towards living to eat, instead of eating to live. It is not only the wealthy and leisured who are guilty in this respect. The use of food accessories has largely extended throughout all classes.

In the present volume an attempt has been made to describe in a brief compass the general laws governing digestive processes in all living bodies. A study of these processes as carried out in plants and in lower animals serves to indicate the modes and means by which living protoplasm in all vegetable and animal cells can most easily and economically procure a "living wage." The higher animals only differ physically from the lower in being formed of myriads of living cells which have as it were joined a "Trades Union" to enable them to assist each other in the most economical and thorough way, and have for the most part abandoned individualism. Should conditions exist under

which the cells in any section of this "Trades Union" are afforded an insufficient wage, their action resembles the "strike" of human members of similar bodies. As their income is given them in kind, not in money, the deficiency may take various forms and affect either one section of the cells of the body or the whole number present in it. For instance, should the cells of the stomach or liver be given too much to do, they often strike for shorter hours and longer holidays; if too little iron be available to pay the red blood corpuscles, or perhaps too much lost to them by leakage from the body, they very soon indicate their wish for a greater supply, or for lessened expenses. The food and air taken in are the paymasters, and if they are unable to grant the amount demanded, stoppage of work ensues; perhaps temporary, perhaps permanent. As cellular units are built up from the elements of the food accessible to them, and as the nature of the food influences their state of well-being, though not necessarily their physical and inherited form, animal and vegetable bodies, forming collective groups of cells, are as dependent upon the elements given them in food as any single-celled representative of individualism.

No animal can change his generic form by altering his food, but he can modify, often very profoundly, the attributes of his component cells. But even this is not invariably the case, for some men develop great strength of mind and body on a vegetarian diet (*plus* milk and eggs), while meat always disagrees. In hot climates much meat is harmful, but experience teaches that the more meat eaten by the inhabitants of a temperate clime the greater is their brain power and physical prowess. The great nations of the earth exemplify this very clearly. I have perhaps stated in the text the case against the professional vegetarians—not against those induced or compelled to use such a diet from personal idiosyncrasies—in rather too dogmatic a fashion, but we have only to consider the dentition and structure of the alimentary canal in man, and to recall the very varied conditions under which he has from time

to time lived, to be assured that the beautiful fantasies conjured up by such enthusiasts, in which man appears as a frugivorous and herbivorous animal shedding no blood to gratify his carnal appetite, have little solid basis for their support.

The course of history has been and still is controlled by the diet of the nations. The present struggle for commercial supremacy is largely a matter of digestion. The British workman, better fed and eating more meat, works more rapidly and more energetically than many of his continental confrères; but working a shorter time and earning higher wages, his standard of diet and dietetic accessories is rising still higher and is exceeding the small margin of profit left by his more rapid working or greater skilfulness. However much the food of one man succeeds in developing his power of action above the capabilities of another subsisting on a poorer diet, there must be a point at which the shorter and shorter hours and the increasing pay of the first must become unable to produce the equivalent of the work of the other, who works longer hours for lesser pay, even though less skilful. The appetite grows with what it feeds on; the worker having once experienced the benefits of a generous diet, craves for more and more, not realising that a narrow line divides the diet best adapted for brain and brawn from the slightly richer diet, which yields to the body rather greater income than suffices to balance its current expenses, and may lower all the bodily functions to a point below that appertaining to the slightly under-fed but not ill-fed individual.

But to return to the book itself: I take the opportunity of warmly thanking the Royal College of Physicians of Edinburgh for the leave granted me to prosecute original researches in their laboratory, and of expressing my indebtedness to Dr. Noël Paton, the superintendent, for much kind advice and guidance. In all cases the name of the authority for any dogmatic statement has been inserted in the text, and in the more interesting passages the reference given, but it was deemed of very little use to include a bibliography of all the

works consulted, as such could not be complete without the addition of many unquoted papers, while those who desire to investigate the literature of the subject more fully can obtain every important reference to it from such comprehensive works as the *Index Medicus*, Schmidt's *Jährbucher*, or from the catalogues of any of the larger medical libraries. Much information may be derived from the perusal of such standard works as:—on historical subjects, Baas's *History of Medicine* and Withington's *Medical History from the Earliest Times;* on the physiology of plants, Sachs's different works, especially his *Lectures* on this subject (in German, English translation by Marshall Ward), *The Natural History of Plants*, by Marilaun (English translation by Oliver), Darwin's *Carnivorous Plants*, and Geddes's article on "Carnivorous Plants" in the *Encyclopædia Britannica*, appended to which is a full bibliography of the subject; on the physiological processes in animals, Meade Smith's *Physiology of the Domestic Animals;* the text-books on human physiology by Michael Foster, Stewart, and Waller; on physiological chemistry by Neumeister (in German), Bunge, Gamgee, and Hoppe-Seyler; on diet and indigestion, Sir William Roberts's *Diet and Digestion*, Lauder Brunton's *Disorders of Digestion*, and Knight's *Food and its Functions.* From these books much information may be gathered, while Uffelmann and Munk's work on nutrition (German) will give some of the more technical details.

The majority of the illustrations have been borrowed from previous works, to the authors and publishers of which I am deeply indebted. My thanks are due for this permission to Professor Schäfer and Messrs. Longmans, Green & Co., for several figures from Quain's *Anatomy;* to Dr. Meade Smith, the author, and F. A. Davis, of Philadelphia and London, the publisher, of *The Physiology of the Domestic Animals;* to Mr. R. Francis Nesbit and the proprietors of the *Strand Magazine*, for permission to reproduce four plates; to Mr. H. J. Veitch and the Royal Horticultural Society, for two figures; and to Dr. Lovell Gulland, for the use of one photo-

graph and four original figures of the microscopic appearance of the gastric epithelium and zymogen granules in the fish.

The drawing showing pepsinogen granules in the gastric cells of the salmon is, I believe, the first representation of the actual peptic zymin ever published. The original has just appeared in a Report to the Fishery Board of Scotland, referred to on page 254. For valuable assistance when photographing the movements of *Drosera* under difficult conditions I am indebted to Mr. J. Hume Paterson, assistant in the Royal College of Physicians' Laboratory, Edinburgh.

Most of the charts are original; one or two have been modified from diagrams previously published, the others constructed from original data, or from data the source of which is in each instance acknowledged.

A. L. G.

EDINBURGH, *May* 1898.

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ERRATA.

Page	103,	line	9,	*for*	"aggregations"	*read*	"aggregation."
,,	196,	,,	7,	,,	"glycoxylic"	,,	"glyoxylic."
,,	256,	,,	6,	,,	"Canals"	,,	"Canal."

TEMPERATURE.

To convert degrees Fahrenheit into degrees Centigrade, subtract 32, multiply by 5, and divide by 9.

To convert from Centigrade to Fahrenheit, multiply by 9, divide by 5, and add 32.

THERMOMETRIC SCALES.

	Centigrade.		Fahrenheit.	
	100°	Boiling point	212°	
	95°		203°	
	90°		194°	
	85°		185°	
	80°		176°	
Serum albumin coagulated	75°	Serum globulin coagulated	167°	Activity of unorganised ferments destroyed.
	70°		158°	
	65°		149°	
	60°		140°	
Stearin melts	55°	Myosinogen coagulated	131°	Activity of ferments greatest.
	50°		122°	
	47°	Paramyosinogen coagulated		
Palmitin melts	45°		113°	—Body temperature in birds.
	40°		104°	
	37°	Body heat	98.4°	
	35°		95°	
	30°	Heat of uncovered skin	86°	
	25°		77°	
	20°		68°	
	16°			
	15°	Temperature used in testing volumes	59°	
	10°		50°	
	5°		41°	
	4°			—Density of water greatest, 39.2°.
Olein melts	0°	Freezing	32°	
	− 5°		23°	
	− 10°		14°	
	− 15°		5°	
	− 17.78°	Zero	0°	
	− 20°		− 4°	

Comparison of the British and the Metric System of Weights and Measures.

WEIGHTS.

METRIC.	BRITISH.	BRITISH.	METRIC.
1 Milligramme (0.001 grm.) =	0.0154 grain	—	—
1 Centigramme (0.01 grm.) =	0.1543 grain	—	—
1 Decigramme (0.1 grm.) =	1.5432 grain	1 grain	= 0.0648 gramme
1 Gramme =	15.4323 grains	1 ounce	= 28.3495 grammes
1 Decagramme (10 grm.) =	154.3235 grains	16 ounces (1 pound) =	453.592 grammes
1 Hectogramme (100 grm.) =	1543.235 grains or 3.5273 ounces avoirdupois	14 pounds (1 stone) =	6.35 kilogrammes (6350 grammes)
		1 Hundredweight =	50.8 kilogrammes
1 Kilogramme (1000 grm.) =	35.273 ounces or 2.2046 pounds	1 Ton	= 1016 kilogrammes

MEASURES.

METRIC.	BRITISH.		BRITISH.	METRIC.
1 Micromillimètre =	0.00003937 inch	..	1 inch	= 2.5399 centimètres
1 Centimètre =	0.39371 inch	..	1 foot	= 30.4794 centimètres
1 Mètre =	39.37079 inches	..	1 yard	= 91.4383 centimètres
1 Kilomètre =	39370.79 inches or 0.6213 mile	..	1 mile	= 1609.315 mètres

To convert centimètres to inches, multiply by $\frac{13}{33}$.

To convert inches to centimètres, multiply by $\frac{33}{13}$.

VOLUME.

METRIC.	BRITISH.	BRITISH.	METRIC.
1 Centimètre cube (Cubic centimètre) =	0.061027 cubic inch	1 fluid ounce	= 28.3968 centimètres cube
		1 pint	= 567.9 centimètres cube
1 Litre (1000 c.c.) =	61.027 cubic inches (35 fluid ounces, or 1.75 pint.)	1 cubic foot	= 28.315 litres

ENERGY (Approximate).

METRIC.	BRITISH.	BRITISH.	METRIC.
1 Kilogrammètre =	7.24 foot-pounds	1 foot-pound	= 0.1381 kilogrammètre
1 Kilocalorie (of heat) =	3069.036 foot-pounds	1 foot-ton	= 310.00 kilogrammètres
		1 Kilocalorie (of heat)	= 423.9 kilogrammètres

THE NATURAL HISTORY OF DIGESTION.

CHAPTER I.

Ancient Theories of Digestion.

In Animals:—Uncivilised Man—Demonology—Ancient Egypt—The Hindus—The Chinese—The Greeks—Hippocrates—Coction—Plato—Dogmatic School—Aristotle—Alexandrine School—The Empirics—The Romans—Asclepiades—Galen—Mediæval Europe—Arabic School—Paracelsus—Iatro-chemical School—Iatro-mathematical School—The Eclectics—Animism—Nervous Pathology—Vitalism—Phlogistics—Brunonian System—Chronological Synopsis.

In Plants:—Theophrastus — Dioscorides — Doctrine of Signatures—l'Ecluse—Linnæus—Hales—Ingenhouss—von Liebig and Boussingault—Schulze—Pasteur—Sachs.

I.—ANCIENT THEORIES OF DIGESTION IN ANIMALS.

Any survey of the views held by mankind in the past on the subject of animal digestion and bodily nutrition must necessarily be synonymous with the history of medical science. The savage, or the rudely civilised man, cannot fail to speculate on the causes which underlie his sensations of hunger and thirst. The great business of his life consists in the search for food to satisfy the one, and for water to quench the other. He is, however, more impressed by any interference with the functions of the body than by the *rationale* of processes which in health give little sign of their existence. To him health is an abstract, disease a concrete idea.

The majority of ancient medical records which have come

down to us are largely occupied with references to diet and descriptions of imaginary causes of ill-health. In the absence of direct testimony as to the conceptions held by the ancients with regard to the manner in which the food they ate nourished their bodies, we are forced to rely on statements throwing a side-light on the general subject.

The inhabitants of ancient Egypt believed that all diseases arose from food, and they followed precept by practice in taking a purgative and an emetic regularly three times a month. They regarded sensations of hunger and thirst as quasi-poisonous substances which forced themselves into the body, and required to be subdued, or neutralised, by the taking of food or drink to save the body from destruction. Even the dead were supplied with food to shield them from any inconvenience caused by such sensations. Apart from this, the Egyptians were careful of their digestion, observing strict dietetic rules, many of which can still be read in the *Ebers Papyrus*, probably the oldest medical book extant, dating from about 1550 B.C.

The prevalent idea that diseases were due to the entrance of evil spirits, or demons, into the body is well illustrated in the Apocrypha by the story of Tobias. It is there related that Tobias, wishing before his marriage to exorcise a demon which had taken possession of his bride, fumigated her with the burning heart and liver of a fish. The smell thus arising drove the demon away to the furthest parts of Egypt! This demonological view of disease can be traced in many parts of the biblical narrative, and has survived up to the present date among the ignorant in all countries. The demon was considered of a sufficiently substantial form to require some other habitation after his expulsion, a process of reasoning which we may observe in the New Testament story of the herd of swine. A curious instance of similarity in ideas at very different periods is afforded by the supposition of the Hindus that the demon of a disease such as jaundice, causing a yellow colouration of the skin, sought a bird of yellow hue to inhabit after its expulsion from the body, a supposition which was closely paralleled by the much later doctrine of "Signatures."

The authors of the great epic poems of the Hindus have given evidence, however, of the existence of other theories related indirectly to demonology, whereby principles or humours were supposed to reside in the body and to direct

the natural digestive processes. Thus the Aryan writers recognised three principal humours:—

Vata, situated between the feet and navel, or Wind.

Pitta, between the navel and heart, or Bile.

Kafa, between the heart and top of the head, or Phlegm.

The principle, *Kafa*, was predominant during the period when the food was in the mouth; *Pitta*, during the course of digestion; and *Vata*, after the food in the stomach was fully digested. If from any cause these principles became unduly prominent, the condition of the bowels was affected. Thus when *Vata* exercised too strong an influence the bowels were costive; when *Pitta*, or the bile, was in the ascendant, they were loose, while they acted normally when *Kafa* was the most powerful.

These writers describe also a *Pachaka*, or fire of digestion, situated between the stomach and small intestine, which assisted digestion and imparted heat to the body. *Pachaka* was able as well to separate the nourishing portions of the food from the dejecta. By some this body was looked upon as being identical with *Pitta*, or bile, and the author of the *Rava-pradipa* imagined it to be a minute heating substance situated in the centre of the navel. Another principle was supposed to reside in the liver and spleen. This *Ranjaka* imparted redness to the essential fluid of the body, changing it into blood.

The changes which foods and medicines underwent from contact with the digestive fire were termed their *Vipaka*. They were thought to become decomposed, although often recognisable in other forms, and their medicinal effects greatly modified. The actions described under the name of *Vipaka* were evidenced by changes of taste. Thus the six kinds of tastes were, sweet, sour, pungent, saline, astringent, and bitter. The first three remained unaltered, and each characterised a *Vipaka*. *Sweet Vipaka* changed saline substances into sweet, promoted phlegm, and lessened wind and bile. *Sour Vipaka* increased bile, and diminished wind and phlegm. *Pungent Vipaka* altered astringent and bitter substances, giving them a pungent taste, gave rise to disorders of wind, but subdued the principles of bile and phlegm. That is to say, the change undergone at the hands of the digestive fire under the influence of *sweet Vipaka* increased *Kafa*, or phlegm, situated in the body above the heart; when *sour Vipaka* acted, *Pitta*, or the bile, placed

between the navel and the heart, caused symptoms of disease or discomfort; while *pungent Vipaka* increased the principle resident below the navel, *Vata*, or wind. The external elements which brought about the changes in the principles were five in number, ether, fire, air, earth, and water.

The literature of the Hindus abounds with references to medicine and the proper treatment of disease. The *Rig-Veda* (2000-1000 B.C.) and the *Atharva-Veda* (700 B.C.) contain many passages relating to herbs, diseases, and healing waters, but are mainly concerned with incantations and invocations for use against the demons of disease, or for the help of the deity presiding over the organ affected. Their dietetic rules were extremely minute. Meat was generally forbidden.

Among the Chinese the medicine and physiology of yesterday are the same as that of to-day, and probably will be the same to-morrow. Physiological science is at its lowest among them. The principle of "moisture" is located in six chief organs, the heart, lungs, spleen, liver, and the two kidneys; "warmth" in the stomach, small and large intestine, gall-bladder, and urinary apparatus. These two fundamental principles, warmth and moisture, whose union is life, whose separation is death, are associated in the Chinese mind with two elements, wood and metal, analogous to the fire and earth of the Greeks. The blood flows out from the lungs five times daily, terminating in the liver. They regard the bile as the seat of courage; the spleen, of reason, and, with the assistance of the heart, of ideas; the liver as the granary of the body, and the stomach as the abode of the mind!

From an early period the stomach was generally recognised as the chief organ concerned in digestion, and the earliest writers on medical subjects paid much attention to it. The Greeks of antiquity supposed that food putrified, or was cooked, in it. Anaxagoras of Clazomenæ (500-428 B.C.) imagined that the body by means of affinity made use of the results of this digestion by appropriating those portions akin to itself. The great Hippocrates favoured the idea that gastric digestion was a process of coction, in which heat brought about the necessary changes in the food. He (460-377 B.C.) was the forerunner of what is called the Dogmatic School, or, as Galen said, the founder of the Rational School, the legitimate ancestor of modern scientific medicine. This school held that the science of medicine should be based upon the study of anatomy

and physiology. If its members had not attempted to rear a complete structure of medical science before obtaining a sufficiently sound foundation of physiological data on which to rest it, they might have arrived even at that early time at results not far removed from those of the present day. Hippocrates separated the active agents of the body into four principal humours, blood, phlegm, black and yellow bile, as other Greeks had done before him. Heat, cold, dryness, and moisture were their corresponding qualities. Heat, due to the blood, caused digestion of the food. The liver formed blood and bile, and assisted the process of coction in the stomach by increasing its heat. To certain foods were ascribed qualities corresponding to the four humours, and such foods were recommended for maladies due to excess or defect of humours. Dietetics, as a science, was founded by Hippocrates. The following extract from Baas, in Handerson's translation (New York: Vail & Co., 1889, p. 102), sums up his views on this subject:—

> "This science regarded the age—'Old persons use less nutriment than the young,'—the season—'In winter abundant nourishment is wholesome; in summer, a more frugal diet,'—the bodily condition—'Lean persons should take little food, but this little should be fat; fat persons, on the other hand, should take much food, but it should be lean,'—the habits, etc. In addition, respect was paid to the easy digestibility of food—'white meat is more easily digested than dark'—and to its preparation. Water, barley-water, and wine were recommended as drinks. Baths, inunction, gymnastic exercises, and the frequent use of emetics were also commended as dietetic measures, and the dietetic principles of Hippocrates in febrile diseases are substantially observed at the present day."

Immediately following Hippocrates came Plato the philosopher (427-347 B.C.). As so often happens, the enunciation of a rational doctrine by Hippocrates tended to cause a reaction, through which men were led to seek for the underlying principles of physiology and disease, not by the study of facts, nor the evidence of the senses, but in purely mental speculations. Reflection ranked higher than experience. The hold which this method of solving physical problems obtained on the physicians and thinkers of that time put back the advance of physiological knowledge by a period only to be reckoned by centuries Plato, for instance, gravely propounded the theory that some of the fluid drunk passed through the wind-pipe into the lungs, and there served to cool the heart. Taste, he said, was due to the conveyance of soluble, sapid

atoms to the heart and soul by small vessels; the intestinal tube was long and tortuous, so that the food might not have to be renewed too often and thus incommode the contemplations of the soul; the spleen was the abode of blood impurities, the liver of the lower desires.

Based upon Plato's fantastic and speculative scheme of humoral physiology and pathology, which disregarded the analytical portion of the scheme of Hippocrates, was founded the Dogmatic School. Praxagoras of Cos, one of their number (*circa* 335 B.C.), specified no fewer than eleven humours. He regarded digestion as the outcome of putrefactive processes, and recorded the first known case of *bulimia*, or inordinate appetite. His treatment of intestinal obstruction, as told by Cælius Aurelianus, exhibits evidence of a very correct knowledge of the functions of the bowel. He recommended purgatives, enemata, emetics, injections of air *per anum*, or, if these failed, massage of the abdominal walls, and finally laparotomy, with division and suture of the intestine.

Aristotle (384-321 B.C.), in addition to philosophical works, wrote many valuable treatises on natural science. He was the first comparative anatomist and physiologist. Although his influence among physicians and medical scientists was not so great as that of Plato, he did much to break down the excessive idealism current in the latter's system, and to bring back thought into more realistic grooves. Plato's system, however, appealed more strongly to men's imaginations, and long served to dominate the truer science of Aristotle. Like the "Father of Medicine," he regarded digestion in the light of coction in the stomach, the resulting chyle proceeding to the heart. He looked upon the blood as the medium by which the nutritive material for the growth and warming of the body is conveyed through the vessels, containing in its normal condition neither mucus, black or yellow bile, nor water.

Herophilus (*circa* 335-280 B.C.) and Erasistratus (*circa* 330-280 B.C.) were the founders of the Alexandrine School, and the most celebrated members of it. They, however, differed widely in their tenets.

Herophilus discovered the chyle duct, the lymphatics, and the duodenum, which he named, and described the liver accurately. He was a follower of Hippocrates and of the humoral doctrine. Erasistratus also was acquainted with the lymph and chyle vessels, which he said contained air and milk

alternately. He, however, discarded the humoral system, and propounded one of his own, based upon the theory that the arterial vessels contained "vital spirits." He ascribed digestion to the result of friction of the food between the stomach walls (see Iatro-mathematical School, p. 12), nutrition to the addition of new particles, and secretion to the action of what he termed the non-attractive force. He thought that the bile was useless, the spleen superfluous, and showed that fluids did not enter the air passages.

The Empirics, among whom was Heraclides (230 B.C.) of Tarentum, despised anatomy and physiology, saying with Serapion, "It is the cause, not the cure of diseases, that concerns us; not how to digest, but what is digestible." Among the few fragments of a book written by Heraclides, *On Diet and Health*, we find such suggestions as that it is always well to eat a little before drinking, and that sheep's trotters, snails, and other glutinous substances will cause dyspepsia if eaten to excess.

Few records have come down to us of the medical opinions current among the inhabitants of early Rome. They believed that all the organs of the body were supervised by special divinities, who could be appealed to if anything untoward occurred. Asclepiades of Prusa (about B.C. 200), a Greek physician who had studied in Alexandria and Athens, was the first physician of importance. He introduced a new doctrine into physiology, founded on the atomic philosophy of Democritus and Epicurus. He looked upon the body as composed of atoms, with canals or "pores" between them in which still more minute atoms circulated. Disease was caused by changes in their relationship, and by blocking of the pores.

Of Asclepiades and his views on digestion Celsus notes, "And there are rivals of Asclepiades who suggest that all these [pores] are useless and superfluous; for nothing is digested, but from the crude material, such as is ingested, everything in the body is derived."

It is probable, however, that Cicero expresses with more truth the opinions of Asclepiades, whose personal friend he was, in the following words:—"In the alimentary canal many wonderful processes take place; . . . the bowel also, owing to its complex and tortuous form, holds together and arrests the material introduced, whether it be dry or moist, and thus

it is able to alter and digest it; then contracting and relaxing it, curdles and mixes everything it receives, so that both by the action of heat, of which it has much, by disintegration of the food, and further, by the aid of the 'spiritus,' all is distributed throughout the body, concocted (prepared) and digested."

The most famous of all the Roman physicians, Claudius Galen of Pergamus (A.D. 131-201), is worthy of more particular notice, for the world during more than a thousand years followed, more or less implicitly, his teaching and doctrines. He is classed by some as belonging to the Dogmatic School, by others among the Eclectics. He himself denied any association with the Eclectics. Following Hippocrates and the Alexandrines, he emphasised the great importance of the study of anatomy and physiology, and as he performed many experiments in both of these sciences, his opinions are of great interest. He regarded bodily metabolism as the outcome of the actions of the four elements, water, air, fire, and earth, to which pertained the qualities of moisture, coldness, warmth, and dryness respectively. Thus water constituted the major part of mucus (cold and moist), which was chiefly formed by the brain; fire predominated in the yellow bile (warm and dry) originating from the liver, earth in the black bile from the spleen (cold and dry), while the blood contained the four elements equally mixed (warm and moist). Digestion of the food was brought about in the stomach by means of coction; the results of digestion went to the liver, where they became blood (an error which persisted up to the seventeenth century). The blood, on reaching the heart, was driven by part of that organ to all portions of the body, and was almost entirely used up in transit in their nutrition. There can be no doubt that the extraordinary error made by Galen in the ascription of the formation of the blood to the liver, and the origin of the veins to the same organ, hindered him from discovering the circulation of the blood. A convincing token of his acuteness is afforded by his suggestion that respiration serves to heat the blood, not to cool it, as was generally believed in his time, while he even theoretically discovered oxygen by postulating the probable existence of an element in the air which might be the source of this heat.

Aretæus of Cappadocia (A.D. 30-90), an earlier member of the same school, believed that the blood was prepared in the liver,

the bile in the gall-bladder, and that a secondary digestion took place in the large intestine.[1]

That even Galen, the chief authority in medical science for over a thousand years, had peculiar ideas about the nature of digestion is shown by his statement to Marcus Aurelius, who was suffering from dyspepsia. When asked what was amiss he explained that he suffered from a digestive disorder due to the food he had eaten, which required to be turned into *phlegm* before being excreted. Little of interest or of value can be gathered from the writings of those who followed Galen. For a period to be measured by centuries the current opinions were only variants of Galen's views. In the dark ages of mediæval Europe the tendency of all knowledge was rather to recede than to advance; indeed, the influence of Christianity tended to hasten the decline of medicine rather than advance its progress. The majority of the treatises which have come down to us from that time deal mainly with diet, often in what may seem to us ludicrous ways. Two of the physicians who flourished in Constantinople in the eleventh century are, however, worthy of mention. Demetrius Pepagomenus wrote an excellent monograph on gout, in which he

[1] The following rock inscription, found at Epidorus, and quoted by Miss Jane Harrison (*Brit. Med. Journal*, 17th July 1897), affords a good example of contemporary tenets:—"M. Julius Apellas, who was suffering from many complaints and from attacks of indigestion, was sent for by the god, but on the journey when I was at Arginia he bade me not be so nervous about myself. And when I was come to the precincts, he bade me go about for two days with my head covered. I was to eat bread and cheese, a salad of celery with lettuce. I was to attend to myself in the bath and to drink lemonade, rub myself against the wall of the bath, take exercise in the loggia, practice on the trapeze, rub myself with sand, and go barefoot, pour wine into the hot water of the bath before I got in, bathe myself alone and give the bath attendant an Attic drachma, making offerings to Asklepios and Epione and the Eleusinian goddess in common, and drink honey mixed with milk. And one day when I was drinking milk alone the god said to me, 'Put honey in your milk that you may be easier of digestion.' When I prayed the god to heal me more quickly I felt as if I was rubbed all over my body with salt and mustard, and was going from the shrine to the baths, I saw a youth with a smoking censer, and the priest said: 'Your cure is accomplished, and now you must pay your fee.' I stayed on still longer and he bade me use anise and oil for my headache, but just then I had no headache; however it happened that from working too hard I got a rush of blood to the head. I used the oil and my headache went. He ordered me to gargle with cold water for a swelling in the glands. He ordered me also to make up the record of this. Cured and grateful I have departed."

declares that it should be treated by diet rather than by drugs; a method which, as he confesses, is easier to advise than to adopt. John Actuarius recommended that ointments with purgative ingredients should be rubbed into the skin, showing that he knew of the central action of many of these substances, although it is doubtful if he understood their mode of action when thus applied.

Among the celebrated leaders of the Arabic School of Medicine we find Isaac Ben Solomon (850-950), who lived in Egypt and wrote many highly prized works. A quotation from his work on *Diet* may prove interesting.

"The flesh of pigs is most nutritious; it forms a good chyme, and by its humidity and viscosity preserves the moisture of the stomach. It is diuretic and not suited to those who eat little. It is useful for those of hot and dry temperaments, for they readily digest and thrive upon it; but for those of an opposite complexion and of weak digestion it is noxious, generating evil humour and a viscid phlegm, which may produce gout, lumbago, sciatica, renal stone, and paralysis. The flesh of old and decrepit pigs is most unwholesome; it is hard, woody, insipid; those who habitually eat it fall into melancholy and hectic fevers" (quoted by Withington, *Medical History from the Earliest Times*, p. 149).

Another physician of this school, Averröes, the son of the great Avenzoar, gives in one of his books the following philosophical description of barley-water and its uses:—"Barley bread is inferior to wheaten, but is cooling and readily digestible, and its coldness is of the first degree. Barley-water is more medicinal than the bread; it is excellent in hot and dry diseases, since it cools, moistens, tempers and wonderfully generates a laudable humour. Nor does it inflate or remain in the stomach; all this we have learnt from experience" (Withington, *loc. cit.*). Then follows a minute description of the proper mode of preparing it.

Some peculiar statements on diet by a much later Arabic physician, Arnald of Villanova (1235-1312), may be quoted here to afford an idea of the advice given in those days to patients. "Let him take moderate exercise before eating, and rest entirely after it, till the food has left the stomach, and then ride horses or gently trotting mules." "He may sleep soon but not immediately after eating, and should lie first on the left side that the food may descend to the fundus of the stomach,

and then on the right that it may pass on." He may eat among other things pickled pork, but only rarely. In winter and spring he should take two meals a day, but three smaller ones in summer. He should never eat until he has fully digested the previous meal, "for nothing is worse than to add indigestion to indigestion."

At the dawn of the Renaissance physiology and other medical sciences again began to develop, although they were among the last of the sciences to be affected by the revival of learning which began in the middle of the fifteenth century. Perhaps we may say that nearly a hundred and fifty years elapsed from the year 1413—when a long-lost book of Celsus, *De Medicina*, was discovered, and started a spirit of research into the history of ancient times—before the sciences of physiology, chemistry, and medicine really felt the influence of the age of reformation in its entirety.

Theophrastus von Hohenheim, or Bombastus Paracelsus, as he is otherwise called (1493-1541), was one of the best known of the physicians of that period. We may only note in passing, however (for his reputation was much higher than his merits), that he looked upon digestion as carried out by a presiding force in the body, which he termed its "archeus." This force separated the nutritious from the poisonous ingredients of the food, and helped to absorb the nutriment. If the "archeus" failed in his duty, or if the excretory organs were unhealthy, the poisonous part of the food remained in the body, meeting with "a spirit of coagulation," which caused its deposition as tartar on the teeth, or as gouty deposits in the joints. The archeus of Paracelsus seems to have been a reminiscence of the demonology of the ancients, and to have caused the digestion of food solely by means of heat.

Johan Baptista van Helmont (1577-1644) was the first to look upon digestion as a process of *fermentation*. He, indeed, bound up his theory with the doctrine of material life in such a way as to appear ludicrous to us, but he deserves credit for being one of the earliest to break through the artificial fabric of medical science erected by Galen and his successors. To him the whole body was under the influence of an "archeus influus," or vital principle, which resided in the stomach, while every organ had its "archeus insitus" directing the processes natural to it. During the process of digestion in the stomach the local "archeus" generated a ferment whereby

an acid was produced to dissolve the food. This "fermentum acidum" caused the necessary changes to take place in the food, not by means of heat, but by some other vital action. Van Helmont was aware that acids alone are unable to act as digestive agents, but require the additional aid of a ferment. He was unable to explain this action in a satisfactory manner, but summed up the properties of his ferment as follows:— "A digestive ferment, therefore, has the essential power, by reason of its vital acidity, of causing transmutations." Such men as Sylvius, Descartes, and Willis belonged to this school, and identified gastric digestion with fermentation.

Nehemiah Grew (1628-1711) wrote shortly on digestion at the end of the seventeenth century, and notices the glands in the mucous membrane of the stomach. The following quotation from a lecture by him is given in Gamgee's *Physiological Chemistry*:—"By the joynt assistance of the glandulous and nervous membranes the business of chylification seems to be performed. The mucous excrement provided by the former, as an animal corrosive, preparing, and the excrement of the nerve by the latter, as an animal ferment, perfecting the work."

Following the inconclusive attempts of the chemical school to attribute natural processes to purely chemical operations, another school of physiologists arose. The Iatro-mathematical School based the phenomena of digestion and other physiological processes upon the action of mechanical laws, in some cases admitting the co-existence of chemical changes. Their study of the mechanical attributes of the different parts of the body resulted in many and lasting additions to science, even although many of their notions were extremely extravagant. Borelli (1608-79) and Redi (1626-98) may be mentioned as leaders of the school, the latter of whom studied the mechanism of the gizzard of birds very carefully. The mechanical action of the gizzard probably suggested the idea of a similar action by the gastric walls in man.

As an example of the extraordinary lengths to which disciples of the Iatro-mathematical School ventured to go, I may cite the argument used that, as the pressure capable of being excited by the human thumb is very considerable, and as the superficies of the stomach wall is much more extensive, so the pressure which can be exercised by the coats of that organ is correspondingly greater. Dr. Pitcairn estimated this power at 12,951 pounds, or about five tons, and ascribed gastric digestion

to this triturating force alone, a force greater than is generally applied by large millstones. In his essay he states that this explanation is quite sufficient, and that there is no need to call in "the assistance of a Dæmon or a Stygian Liquor."

The Eclectic System originated with Hermann Boerhaave (1668-1738), who combined in it many of the doctrines of earlier systems. Among other tenets, he held that the acridities of the body fluids played an important part in the functions of life. There were acid, saline, oleaginous, glutinous, alkaline, and mixed acridities originating from the food and causing disease. Digestion of food was ascribed to mechanical forces.[1]

Under the name of Animism, Georg Ernst Stahl (1660-1734) ascribed the force used in digestion, along with all the other bodily processes, to the "soul," or supreme principle. It was not the same as the spirit, but the special life-giving and life-preserving principle of the body.

William Cullen (1712-90), reasoning by pure deduction, laid the foundation for modern Solidism in his system of Nervous Pathology. Disregarding all the fanciful principles and forces so often stated to exist in the fluids of the body by the authors of earlier systems, he founded his system on the living solid parts, aided by the nerves. The presiding force over the bodily processes he called "the nervous principle."

Another system, that of Vitalism, was introduced by Bordeu, of Montpellier (1722-76), and supported by Barthez, of the same school (1734-1806). In this system the "vital principle" is the cause of all the phenomena of life, carrying on the digestion of food, muscular force, the production of heat, and the mental processes. It is diametrically opposed to our modern conception of force and matter.

The Phlogistic Theory merely treated of animal heat, but one of its supporters, Edward Rigby (1747-1821), held that

[1] *Medicina Musica, or a Mechanical Essay on the Effects of Singing, Musick, and Dancing on Human Bodies*, by Richard Broune, "Apothecary in Oakham," 1729. Of singing, after dwelling on its efficacy in chasing away "dark, gloomy ideas," he says: "Singing must mightily conduce to the Dissolution of the Aliments and Prevention of Crudities and Indigestions, the ill consequences of which are too well known to want Demonstration; the Diaphragm also and abdominal Muscles, by this Exercise compressing the Stomach with more force than ordinary, give more Assistance to the Stomach in Comminuting the Food into Chyle, and rendering it fit for its Translation into the Blood."

the stomach was the seat of "phlogistification,' where free heat was produced.

The Brunonian System (John Brown, 1735-88) was based on the supposition that life was an artificial result of irritations always in action. Irritations cause excitement, to which all the processes of the body are due. They are of two kinds: external, as food, blood, warmth, etc.; internal, as thought, feeling, and movement.

Such were the different systems and theories formulated from time to time by the greatest physicians, scientists, or philosophers of their day. At the present time we are unable to appreciate at their true value the circumstances under which they were formulated, the advantages or disadvantages attendant on their conception. But it must remain an element of surprise and disappointment that the views current up to the close of last century should show so slight an advance on those formulated, with less particular knowledge, two thousand years before. Nor are any of the systems propounded in the days of Hippocrates and his successors less fanciful than many seriously suggested by men of attainment during the eighteenth century.

A no less surprising fact is the immense advance which has been made since the beginning of the nineteenth century in the elucidation of physiological problems. Coincident with the onward progress of science our knowledge of the chemical and physiological processes which serve to support life has increased. Thanks to the patient investigation of the infinitely little, and to the gathering together of the results, theories of vital processes can now be based on multitudes of observed facts, giving both positive and negative evidence.

By following the teaching of Hippocrates in 400 B.C., teaching which was until lately entirely disregarded, or at best spasmodically and superficially followed, we have penetrated many of the mysteries connected with bodily processes, though much still remains to be done.

The outcome of more than two thousand years of inquiry into the manner in which the food is altered in the body so that the nutritious part may be used up and the useless portion cast out, and into the processes by which the nutriment is built up into the various solid and fluid constituents of the organism, may be summed up in one sentence.

The active digestion of nutritive substances results from intimate chemical and physical changes brought about by the action

of a force possessed by the living protoplasm of cells of which we as yet know nothing, but which constitutes the most intimate element underlying that mysterious entity *Life.*

The digestive influence of protoplasmic activity on the food elements may be exerted within the cellular units, or may be applied outside the cell-wall; it may act through direct contact with the protoplasm itself, or be brought to bear on elements not in touch with protoplasm by means of active secretions; and again, a single cell may be capable of all necessary digestive processes within its walls, or groups of cells subordinated to the performance of special digestive functions may serve to support other groups dependent upon them. In the latter case specialised cells are alone able to carry on the processes of actual digestion, although every individual living cell, in virtue of the power inherent in its protoplasmic contents, possesses the faculty of absorbing, and it may be of altering, the substances necessary for its nourishment from the food elements offered it.

Synopsis of the Historical Records regarding Digestion in general.

1550—700 B.C....Demonology: Digestion performed by the aid of a "dæmon," or spirit. Indigestion due to anger of the spirit.—Egyptians, Hindus.

460 B.C............Dogmatic School: Digestion carried out solely by means of heat and moisture.—Hippocrates. Digestion simply putrefaction.—Praxagoras of Cos.

300 B.C............Alexandrine School: The arteries contained vital spirits which performed the bodily functions.—Erasistratus.

220 B.C............The Empirics: Concerned more with what is digestible than how it is digested.—Heraclides.

200 B.C. ....Early Roman: Gastric digestion due to peristalsis (churning movement), mixing, heat, and a spirit or exhalation.—Asclepiades.

1-200 A.D.........Roman: Reversion to Hippocratic teaching, the cardinal qualities of foods, medicines, etc.; heat, cold, moisture, and dryness.—Aretæus, Galen, Celsus.

200-1500..........."Dark Ages" in Europe: No progress made; variants of Galen's views.

850-1312..........Arabian School: Temperaments. Properties of temperature and moisture affect digestion.—Ben Solomon, Avenzoar, Averröes.

1493-1541........."Archeus" of digestion, employing heat.—Paracelsus.

1550-1675.........Iatro-chemical School: Digestion akin to fermentation, under an "Archeus." Gastric juice found to be acid, gastric glands discovered.—Van Helmont, Sylvius, Descartes, Willis, Grew.
1610-1710.. ......Iatro-mathematical School: Digestion chiefly mechanical. —Redi, Borelli, Pitcairn.
1659................Rumsæus uses a stomach brush to remove "mucus."
1664................Graaf obtains pure pancreatic juice.
1710 (*circa*).......Reaumur (1683-1757) obtains pure gastric juice, and finds it acid and antiseptic.
1777 ....Stevens: First demonstration of digestive properties of the gastric juice outside the body.
1783................Spallanzani corroborates the last two observers.
1814................Trevisanus finds a sulphocyanide in saliva.
1824................Prout, and Tiedemann and Gmelin, independently discover the presence of free hydrochloric acid in the stomach secretion.
1825-33...........Beaumont: Observations on gastric digestion in the living subject.
1829................Arnott proposes a stomach syphon.
1831................Leuchs discovers the diastatic action of saliva.
1834................Eberle prepares an artificial gastric juice.
1836................Schwann postulates the existence of pepsin, makes first biliary fistula.
1839................Wasmann isolates pepsin.
1842................Bassow and Blondlot make artificial gastric fistula in the dog.
1846................Claude Bernard: Theory of hepatic glycogenesis, fat-emulsifying ferment in pancreas, etc.
1847................Dubrunfaut isolates maltose.
1851................Heintz finds the milk-curdling ferment.
1851................Lehmann finds lactic acid in gastric contents.
1852................Bidder and Schmidt prove conclusively that hydrochloric acid is secreted by the gastric glands.
1854................Busch finds no secretion in small intestine in absence of stimuli.
Ebstein and Grützner postulate the existence of pepsinogen.
1859................Meissner investigates the products of the gastric digestion of proteids.
1864................Städeler investigates the bile pigments.
Thiry analyses juice of small intestine by means of an artificial fistula.
1871................Paschutin discovers sugar-inverting ferment in small intestine.
Eichhorst shows that ferments are absent in mucous membrane of large intestine.
1873................Liversidge demonstrates the presence of a zymogen of the diastatic zymine in the pancreas.
1875................Heidenhain discovers proteolytic zymogen in the pancreas, etc.
Darwin describes digestion of proteids by plants.

1878 .... Kühne investigates the products of tryptic digestion of proteids.
Richet finds that hydrochloric acid in the stomach contents is often combined with organic bodies.
1881 .... Vella modifies Thiry's fistula.
1882 *et seq.* .... Langley investigates the influence of reaction on the functions of ferments, etc.

II.—HISTORICAL REFERENCES TO THE DIGESTIVE PROCESSES IN PLANTS.

In treating of the historical references to the absorption of nutriment in plants, the fact at once becomes prominent that up to a comparatively recent date no one thought of troubling about the subject. At the present time the average man, "the man in the street," classifies plants into those that are good for food and those that are poisonous, or separates them into those that are pleasing to the senses and those that are unobtrusive or repellent. During the earlier periods of the world's history, owing to the necessity which existed for man to satisfy his hunger, or to supply food for domestic animals, coupled with his inherent sense of that which is beautiful, plants came to be regarded almost entirely from such standpoints. The first trace left us from the past of any endeavour to study plant-life apart from its nutritive or medicinal value is contained in the *Natural History of Plants* by Theophrastus, a book dating from about 300 B.C. Similar books were written by Dioscorides and Pliny. Throughout the whole period of the Roman Empire, and in the dark times of the Middle Ages, no further attention was given to plants save in appraising their value for food or medicine. As an instance, the Doctrine of Signatures, chiefly elaborated by Bombastus Paracelsus, who lived in the earlier part of the sixteenth century (1493-1541), may be mentioned. His doctrine was a species of physical homœopathy; a leaf shaped like the liver cured hepatic disorders, a heart-shaped flower was a specific for cardiac disease. The numerous and bulky herbals published about this time were filled only with the names of plants, and with the authors' endeavours to identify them with those described by the ancients. Their medicinal or dietetic value was estimated solely from adventitious and empirical imaginings.

Charles de l'Ecluse (1526-1609), a Belgian, was the first to study plants for the plants' sake, and the first, also, to travel

for the purpose of botanising. It was the Swedish botanist Linnæus (1707-78), however, who laid the foundations of the scientific study of plant-life. He evolved short and technical names for the different parts of the plant, many of them arbitrary, but none the less useful. The publication of his classification at once gave an immense stimulus to botanical work, and stimulated inquiry as to the reason for and the use of the various organs described by him.

In dealing with the biological significance of the different organs of plants, especially in regard to digestion and assimilation, it would be of little use to refer to the theories of the early philosophers. Aristotle and his school held ideas about vegetable life which are merely fantastic dreams.

In 1718 Stephen Hales published what appears to have been the first series of experiments on the natural history of plants (*Vegetable Staticks, or an account of some Statical Experiments on the Sap in Vegetables, being an Essay towards the Natural History of Vegetation*). It was not till a century later that the secret of nutrition was discovered. Modern science progresses from the individual cell upwards, explaining each step as it goes; previous observers endeavoured to theorise from the functions of the entire plant, and thereby to apportion to each part its rôle in the economy. The enormous strides which have been made in our knowledge of Nature's processes during the last fifty years are the logical outcome of the modern method.

In 1779 Ingenhouss, indeed, proved that carbon, the most abundant constituent of every vegetable body, is obtained from the carbon dioxide of the air; and De Saussure, shortly afterwards, corroborated his statement, and pointed out for the first time the true significance for vegetable metabolism of the mineral matters taken up by the roots. But it was not until Justus von Liebig and Boussingault, in 1840, made renewed and patient studies into the principles underlying vegetable nutrition that these principles could be said to have been thoroughly established or understood, to the immense advantage of agriculture and forestry. Another step in advance was made by Sachs in 1860, when he published the results of his experiments on artificially reared plants, and showed that they could absorb their nutriment from watery solutions without the presence of soil. This discovery

facilitated beyond measure the investigation of vegetable metabolism.

In 1837 Latour and Schwann proved, independently of each other, that yeast cells, known even to Leeuwenhoeck with his primitive microscope, were vegetable cells capable of growth and increase. Schulze, the year before, made the more important discovery that the fermentation of fluids required the presence of minute vegetable organisms, and he showed, and after him Pasteur and Chevreul, that if air be excluded from sterile fluids they remained sterile. The year 1864 saw the publication of the work of De Bary on these organisms. The foundations of bacteriology, so soon to assume a position of immense importance, were thus laid.

More recent years have seen the advent of a host of workers on biological subjects, with an immense amount of literature and an accumulation of so many new facts that space does not permit any historical notice of them in this place.

CHAPTER II.

Digestion in Plants.

General Survey :—Chlorophyll—Formation of Starch—Proteolytic Ferments—In Seeds—Papain—Bromelin—Action of Roots.
Vegetable Metabolism :—Proteids—Carbo-Hydrates—Fats—General Principle—Change in Constructive Materials.
Comparative Digestion in Plants :—Bacteria—Form—Food—Lichens—Algæ—Higher Plants—Cotyledons—Stores of Food—Annuals, Biennials, Evergreens, etc.—Plants flowering only after long periods.

I.—GENERAL SURVEY.

If a seedling of a plant which possesses green leaves, a seedling, for example, of maize (*Zea mays*), be placed in a glass filled with distilled water it will grow vigorously for some time, and may put forth three or four normal leaves (Sachs). As soon, however, as the reserve materials present in the seed are exhausted this growth is arrested, and, although the plant may survive for a long time, it perishes before attaining maturity. On examination of the seed all the proteid and starch formerly present in it is found to be absent. The plant, in fact, has elaborated its leaves from the store of proteid, starch, and salts contained in the seed, with the aid of carbonic acid from the air. On the other hand, if the plant be grown in a solution of various salts, it grows vigorously and continuously. A useful solution for this purpose contains in a litre of water 1 gramme of potassium nitrate and 0.5 gramme of sodium chloride, of calcium and magnesium sulphates, and of phosphate of calcium. In time the small amount of iron in the seed is used up in the formation of the chlorophyll in the first set of leaves, and the later leaves of the plant grown in this solution are quite white. The addition of a small quantity of an iron salt to the solution soon causes the leaves to take on a green hue. A plant

grown under these conditions flourishes normally and can proceed to its full development.

Vegetables bearing green leaves can therefore form protoplasm, proteids, carbo-hydrates,[1] and an inorganic skeleton from such simple substances as those detailed above, provided that a sufficient supply of carbonic acid gas be supplied them from the air.

The roots possess a certain selective power, those of different plants taking up different proportions of salts, but the ash of similar plants contain more or less of a certain salt according as they are grown on a soil rich or poor in it.

The elements necessary for the growth of plants are potassium, calcium, magnesium, iron, phosphorus, and sulphur in suitable neutral combinations containing oxygen, nitrogen in some combined form, usually as a nitrate, carbon in the atmosphere, and hydrogen in water. Numerous other elements, indeed, have been discovered to be present in plants, such as silica in *Equisetaceæ*, iodine in marine plants, and zinc in plants growing on a calamine (native carbonate of zinc) soil, but these are not necessary for the process of nutrition.

In this way plants procure the elements which enter into the composition of proteids in an uncombined state, or in the form of simple compounds, and build up from them the complex proteid molecules. The hydrogen and the oxygen come from water, carbon from the air, nitrogen from nitrates contained in the soil, and sulphur from sulphates. Cultivation of plants in water has shown that nitrates are able to afford nitrogen to the roots, and that the view once held that only ammonia salts yielded nitrogen after absorption by the roots is erroneous. No doubt plants may absorb some nitrogen in this way, but it should be remembered that the ammonia formed by the decomposition of vegetable compounds is easily transformed into nitrates in the presence of potassium or other metallic salts in the soil.

The method by which a plant with green leaves obtains its supply of carbon from the air is a little more complex. The chief agents are the chlorophyll granules. Embedded in the protoplasm of the cells lying near the surface of the leaf many roundish or polygonal granular bodies of a soft consistence may be found. In some of the lower algæ similar structures

[1] For the explanation of the terms, proteid and carbo-hydrate, see p. 136.

take the form of bands or plates. These chlorophyll bodies always lie within the substance of the cell-protoplasm, and possess a bright green colour. If the colouring matter be removed by means of strong alcohol, the bodies still retain their original shape and almost their original size. The colourless matrix responds to the ordinary tests for proteid substances. A chlorophyll granule may therefore be regarded as a portion of the protoplasm of the cell coloured with the pigment chlorophyll. But these granules conduct themselves in many ways like independent organisms; they can grow, change their form, and even divide by fission. The colouring matter itself, chlorophyll, is soluble in alcohol and ether, and is thought to consist of two yellow and two green bodies possessing distinct optical properties. Although the presence of iron is necessary for its formation, that element has not as yet been satisfactorily shown to compose a part of its molecule. It is only developed under the action of light, and its colour varies with the degree of oxygenation.

In the presence of sunlight, chlorophyll is able to detach the carbon from the oxygen in the molecules of carbonic acid gas, to assimilate the carbon, and give off the oxygen in a pure state. The light rays which act in this way are the red and yellow particularly, the blue-violet portion of the spectrum, the active part in photography, having little power of decomposing the gas. The evolution of oxygen and retention of carbon is a function of wave-lengths of light which are not larger than $\frac{69}{2000000}$ mm., or smaller than $\frac{40}{2000000}$ mm. The maximum result is attained with wave-lengths of $\frac{59}{2000000}$ mm. Again, the action of the light on the chlorophyll, and the consequent absorption of carbon and formation of starch, is purely local in character. If parts of the large leaves of such a plant as tobacco be cut off from the light throughout the summer by means of tinfoil, and if, after a few days, a leaf be removed, the chlorophyll dissolved out with alcohol, and a weak alcoholic solution of iodine poured over it, only those portions which had been exposed to the light become blue-black owing to the development of iodide of starch. In like manner, if one part of a leaf be introduced into a space containing air deprived of its carbonic acid gas, no starch develops in it. During the action of light enormous quantities of carbon are daily removed from the atmosphere by the action of chlorophyll. Thus Sachs found that a tobacco plant removed in the course of a hundred

days as much as 400 grammes of carbon, a sunflower more than 800 grammes in the same time. Now 10 cubic metres of air contain little more than 2 grammes of carbon. These two plants alone, therefore, removed as much carbon as would be contained in four thousand cubic metres of air. Weber estimated the production of starch per square metre of leaf surface in *Helianthus annuus* at 5.559 grammes during ten hours of daylight. Such a figure enables one to form a faint idea of the quantity of starch formed and carbon absorbed during the yearly growth of a large tree such as the horse chestnut. Under favourable circumstances the formation of the starch corpuscles within the chlorophyll bodies may be observed by the aid of the microscope. The laminated appearance of these corpuscles is clearly seen to be due to successive depositions of newly-formed starch round the first small portion formed. These starch-grains are rounded, but if they grow out from the periphery of the chlorophyll body, as often happens, the side next the chlorophyll body is more strongly developed. Schimper has also demonstrated the presence of colourless starch-forming bodies in the deeper parts of plants and in their storehouses of reserve materials, as, for instance, in the potato-tuber. These bodies cause the formation of starch by an action of metastasis or transference, not by assimilation, as in the chlorophyll bodies. The actual formation of starch in the latter is probably a very complicated chemical process, not a simple combination of carbon and water in the correct proportions, although the oxygen given off exactly corresponds to that of the carbonic acid used up. It is also probable that the protoplasmic matrix acts on the carbon liberated by the chlorophyll, as starch granules may still be found to increase in some instances after the green colouring matter has disappeared. Sachs suggests that sugar is first formed, and then through protoplastic action it is further converted into starch. The starch thus produced in the substance of the chlorophyll bodies is constantly being dissolved and carried to other parts of the plant. This process continues both in the light and in darkness. As the starch is not formed in these bodies in the absence of light, the process of solution and transportation soon renders them free of it. In daylight the constant assimilation is greater than the removal, and starch accumulates; during the night the stored-up starch disappears.

In some plants, as in the common onion (*Allium cepa*), little or no starch is formed in the leaves, but glucose can be recog-

nised as the immediate result of assimilation. The leaves of *Strelitzia* and *Musa* generally contain fats, not starch, in their chlorophyll bodies, but if grown in a strong light, and with a larger quantity of carbonic acid, they produce some starch. Probably in them the starch is at once transformed into fat. But among the reserve materials proteids are often found, and they are undoubtedly used up in a similar manner. To allow of this, the presence of proteolytic ferments—that is, ferments which are able to change the characters of proteids—must be admitted, and it appears probable that all germinating seeds making use of proteids produce such a ferment. Gorup-Besanez was the first to discover the presence of peptonising ferments in the seeds of the vetch, hemp, flax, and barley. Krukenberg found a similar body in the protoplasm of a myxomycete (*Æthalium septicum*), while many of the bacteria peptonise proteids by the same means. The activity of these ferments in seedlings has been proved by the discovery by Schulze of peptones in the lupine. Particularly energetic peptonising ferments have lately been detected in the latex of *Carica papaya*, and of the common fig, *Ficus carica*, and in the fruit of the pine-apple, *Ananas sativa*. The peptonising ferments in these plants differ from those present in animals in being capable of action in acid, neutral, and alkaline media, and it was thought at the time of their discovery that, owing to this fact, their use in medicine should prove of great service. Unfortunately the results obtained have not been equal to the anticipations, and their action in the animal body does not seem to be so marked as in artificial experiments, and is not to be compared with that of pepsin or pancreatin.

Papain.—The ferment obtained from the juice of the *Carica papaya* forms a fine yellow-white powder. It dissolves with some difficulty in distilled water, almost completely in dilute alkalies and acids. In common with most ferments, its action is greatest at a temperature of about 60° C., but it remains active between 12° and 70° C. Hirsch (*Therapeut. Monatshefte*, December 1894) comes to the conclusion that it is the most powerful peptoniser known in a neutral medium, but that its action on proteid foods is limited. If the proteids are in an indigestible form, as in coagulated white of egg, cooked bacon and ham, and indeed cooked meat of any kind unless very finely minced, its action is nil. It has little action on the proteids of bread, but digests raw white of egg, uncooked

meat, and milk with much vigour. Albumoses and peptone result from its action. In a weak solution of carbonate of soda, or of hydrochloric acid, its power is increased. As compared with pepsin, however, Dott found a marked inferiority. Under like conditions, papain digested with the aid of 0.5 per cent. hydrochloric acid only 12.9 and 11.3 per cent. of raw egg albumin, while pepsin caused the digestion of 99.6 per cent. In an alkaline medium the same observer obtained still poorer results. These experiments, however, were not performed under conditions tending to scientific accuracy. Papain has been found to act strongly on diseased tissues, leaving the surrounding healthy structures unaffected, and is now largely used in the treatment of ulcers, especially in the back of the mouth and nose.

The digestive powers of pine-apple (*Ananas sativa*) have been investigated by Chittenden (*Journ. of Physiology*, xv., 1893). The juice is capable of proteolysis, and the ferment contained in it can act in neutral, alkaline, or in slightly acid media. The juice is acid, its acidity is as high as 0.45 per cent. as hydrochloric acid, and contains albumoses as well as ferments. The principal ferment, which has been named bromelin, can be separated by saturation of the juice with ammonium sulphate, but the product thus obtained always contains albumoses. The ferment may also be precipitated by alcohol and dissolved up in glycerine and water. It acts most powerfully at 60° C., but, like papain, can digest proteids between 12° and 70° C. The peptonising action of bromelin is more closely allied to that of trypsin than of pepsin, even leucin and tyrosin, bodies significant of profound proteid decomposition, occurring in its products.[1] The juice also contains a milk-curdling ferment.

If the precipitate which falls on the addition of alcohol to the juice be dried at 40° C. and used in an artificial digestion experiment on raw egg albumin, its action is found to be slower and weaker than that of pepsin or trypsin.

Thus 0.1 gramme of the precipitate added to a solution of egg albumin had almost no action at a temperature of 40° C. after one hour and ten minutes. 0.05 gramme had a stronger action on half the quantity of albumin in four hours. The following table (Table I.) shows these points :—

[1] Cf. p. 111.

TABLE I.

Reaction of Solution.	Percentage digested by Bromelin. In seventy minutes.		In four hours.
Alkaline, 1 per cent. sodium carbonate - - - -	6.7	...	15.4
Neutral - - - - -	Nil.	...	17.4
Acid, 0.182 per cent. hydrochloric acid - - - -	2.0	...	16.9
Acid, 0.182 per cent. hydrochloric acid with pepsin -	70.2	...	97.0

The reaction of the medium appears to have little effect on the power of the ferment. A glycerine extract of the rind and pulp after expression of the juice also contains some of the ferment, and experiments showed that its action, though slight as compared with pepsin or trypsin, was exerted both in alkalies and acids. The addition of an organic acid, such as acetic acid, produced as much digestion as the addition of hydrochloric acid. Although a considerable quantity of glycerine was used, the acidity of the extract, 0.26 per cent. as hydrochloric acid, shows that the tissues of the fruit of the plant are very acid.

The ferment of the fig (*Ficus carica*) is of a similar nature but has not been thoroughly investigated at present, though Hansen (*Sitzungsber. der Physical. Med. Soc. zu Erlangen*, Nov. 1880) detected it as far back as 1880.

Action of the Roots.—The roots, as we have seen, absorb all the water required by plants (although some ascribe a slight power of absorption to the leaves in many cases), and also procure the necessary mineral salts. The roots themselves have no part in this process. But if the tip of a vigorous rootlet be examined numbers of fine hairs, the root-hairs, may be seen. (Fig. 1.) These are narrow tubes with exceedingly thin walls, and measuring only a few millimetres in length and a few hundredths of a millimetre in diameter. It is through these microscopic hairs that the plant obtains its water, its salts, and its nitrogen. These structures may be regarded as protuberances of the walls of the outermost layer of cells immediately behind the growing tip. They only live for a few days, and as the root elongates the part covered with hairs gradually changes its place in the ground, following the direction of growth. In this way they are able to extract from fresh spots the materials which they are in search of. As each terminal branch of the roots is

covered with thousands of these minute hairs it can be easily grasped how plants are able to procure sufficient water for their growth even in soil which is apparently parched. They in-

FIG. 1.

THE ROOT-HAIRS OF PLANTS (DIAGRAMMATIC).

(From a drawing by the Author.)

A. Terminal branches freed from earth by washing, showing the distribution of root-hairs. *B*. Particles of earth adhering to root-hairs. *T*. Growing tips of the roots free as yet from root-hairs.

sinuate themselves between the particles of soil and absorb the minutest drop of water present. Sachs tried to estimate their power of withdrawing water from a dry soil by determining the

percentage of water in it when the leaves of the plant drooped in a moist atmosphere. He found that a tobacco plant began to droop while the soil, sand and black beech humus still contained 12.3 per cent. of water. This soil was able to retain by adhesion 46 per cent. of its weight of water, so that 33.7 per cent. was at the disposal of the plant; 12.3 per cent. was held too fast to permit of the roots withdrawing it. In a loamy soil 8 per cent., and in a coarse-grained quartz sand only 1.5 per cent. of water remained when the leaves began to droop. These figures show that plants can still withdraw water from the soil when it is impossible to squeeze any out of it. But not only do the root-hairs absorb water, but they possess the power of taking up inorganic solids as well. This property is due to the presence of an acid juice which permeates the root-hairs. The action of this acid on minerals may be well seen by growing plants so that their roots are in close apposition to the polished surface of marble slabs, or of dolomite. After a time, if the slabs be removed and examined, very fine corrosions may be detected on the polished surfaces corresponding to the form of the roots. In this manner carbonates of calcium and magnesium and phosphate of calcium are acted on and the salts altered to a soluble form. Roots are thus by no means only passive agents; they exert considerable force in the withdrawal of water clinging fast to the particles of soil, and in the chemical solution of solid minerals.

The Path of the Absorbed Material.—In aquatic plants fluids and soluble nutritious substances are absorbed by the entire surface, while the evolution of gases from metabolic processes causes condensation of the cell-contents, leading to endosmotic diffusion of fluids into them.

In cellular plants, as in the lichens, mosses, and fungi, the circulation of fluids appears to result from endosmotic action alone.

In a vascular plant the fluid absorbed by the roots, or *sap*, as it is termed, mounts upwards towards the growing parts as a result of endosmotic action, of imbibition or capillary force, and of pressure, constant or intermittent. To endosmosis must be assigned the principal part in the process. The evaporation of fluids from the external surface, even when regulated by the stomata of the leaves, renders the substance of the adjacent cells less fluid, and produces osmotic action, whereby the neighbouring tissues yield part of their

liquid and in turn attract a compensatory flow from the next series of cells; the process continued throughout numberless layers of cells at length exerts an influence on those of the terminal rootlets. Pressure of the cell-walls, partly due to endosmosis, partly to alterations in temperature, serves to propel the fluids in the line of least resistance—*i.e.*, to the upper terminal organs. Herbert Spencer has also attributed to the oscillations of the branches and leaf-stalks or petioles an influence on the ascent of the sap by the intermittent pressure thus occasioned.

In addition to these factors the chemical actions resulting in the formation of starch, its transformation into sugar and the other metabolic processes of plant life, necessitate a supply of water and thus induce its diffusion.

Hales has shown that the sap rises with very considerable force. Experiments on the cut end of branches of the vine showed a force equal to twenty-six inches of mercury. Clarke, also in an experiment on the vine, observed a still greater force. The ascensional force of the sap was capable of balancing a column of water 48 to 50 in. in height. The force exerted by the ascending sap varies with the season and with the hour of the day. It is greatest in spring and during the daytime; the first because of commencing growth, the second owing to the influence of warmth. The chief flow of sap occurs along the elongated cells connected with the vessels in the fibro-vascular bundles.

In spring, before the leaf-buds expand, the absorption of water with its nitrogen and mineral salts exceeds the amount transpired. The excess of water is stored in the stem. After expansion of the leaves in summer transpiration is greater than absorption, and the deficient supply obtained from the roots is rendered adequate by the excess stored in the stem. Even in winter some movement of sap takes place owing to the effect of the higher temperature of the soil than of the air.

Ascending sap is a watery fluid, containing unchanged mineral salts, dextrins, and sugar, but no starch or chlorophyll. When it reaches the terminal and active organs of the plant the element carbon, hitherto absent save in the sugars derived from the reserve stores, is added to it by the process already described. The ascending sap is termed *crude sap*, the sap after the further addition of carbonaceous bodies *elaborated sap*.

There is little doubt but that much of this elaborated sap descends from the leaves to the woody parts of the branches and stem, where it is in part used up in the formation of new tissue, partly in the repair and metabolism of the old, and in part deposited in the form of reserve stores of nutriment. It must not, however, be supposed that the only movements of the sap are in an upward or downward direction. It appears to be able to permeate all the tissues of the plant in any direction, diffusing from one vegetable cell to another. In fact, the walls of vegetable cells seem to allow the dialysis of soluble substances and the diffusion of water to a much greater extent than their analogues in the animal kingdom.

Mulder suggested that the roots assimilate as well as absorb nitrogenous material, and similarly the leaves carbonaceous substances, the movements of the sap conveying these products to all parts of the plant.

II.—THE PRODUCTS OF VEGETABLE METABOLISM.

Before entering upon the description of vegetable metabolism it will be necessary to explain what the term metabolism implies, and to give a brief definition of the substances which take a part in the process. A more detailed account of the different food-elements concerned in metabolic processes will be found in a subsequent chapter. The term metabolism denotes all those processes and interchanges by which a living organism makes use of the inert substances in its food in building up and nourishing its body and in procuring the energy requisite for its bodily activity. Plants are possessed of life as well as animals, and the law of nature, that no kind of action can take place without a corresponding production of energy, applies equally to plants and animals. All living organisms, be they vegetable or animal, are made up of cells, and each active cell is complete in itself as far as vitality is concerned. Every living cell contains more or less protoplasm. Protoplasm is the groundwork of Nature. It cannot be analysed, for analysis implies death, and death occasions intimate changes in its structure. Living it is endowed with the power of initiating structural processes, a power the nature of which is quite unknown to us, while the processes thus initiated serve to form heat and energy with their concomitants, growth and movement. Protoplasm when dead does not differ materially from inert proteid

bodies, and is absolutely incapable *per se* of producing energy. Proteids are complex bodies containing the elements carbon, hydrogen, nitrogen, oxygen, and sulphur in varying proportions, and in addition a small proportion of mineral salts. White of egg is a well-known example of a proteid. A large number of atoms of the elements named go to form a proteid molecule, that is, the smallest portion which contains all the elements in proper proportion and retains the properties of any one proteid. The proteids found in nature or incorporated in protoplasm have relatively bulky molecules, which oppose their easy transit from one part of the organism to another. Proteolysis is the term applied to any digestive process whereby these large inutile molecules are simplified and transformed into smaller and more transportable proteid bodies. In plants simpler compounds are made use of to build up the more complex proteid. They are assimilated, and in virtue of the action of the protoplasmic contents already contained in the cells of the plant are combined together in proteid molecules. Carbo-hydrates form another group of chemical substances which are formed or made use of in metabolic processes. Sugar and starch are the best known examples of carbo-hydrates, which contain no nitrogen, while the hydrogen and oxygen present bear the same proportion to each other as in water—that is to say that the atoms of hydrogen are always double the number of the atoms of oxygen. The only other element present is carbon. Fats contain the same elements but in different proportions. Metabolism of plants is connected first with the formation of these substances from their elements, and secondly with the changes brought about in them so that they may be used in nutrition or employed as sources of energy.

For the proper development of the fungi the five elements contained in proteid matter are necessary, and, in addition, phosphorus, potassium, or one of the metals of that series, and one of the series, calcium, magnesium, barium, or strontium. The higher plants need both calcium and magnesium, the fungi can exist, according to some (cf. p. 37), with only one of them. Iron is not a necessary element. The fungi, as a class, are capable of obtaining the various substances necessary for their growth from a much more widely extended field than the higher plants, and in procuring these substances produce an enormous number of different chemical reactions, some of them useful,

some detrimental to themselves and to others. Dead and decaying matter is a paradise to many of them; indeed they may be looked upon as the scavengers of the world, and as the ultimate transmutation of all living things. The means by which they alter the substances on which they live will be considered in the following section.

Changes in the Constructive Materials in Plants—Ferments.—The starch produced in the leaves may be altered and used at once, or may be stored up for future use. It may be stored up in the form of starch itself, as cane-sugar or as inulin, another form of sugar derived from starch. Cane-sugar and inulin are soluble and are also present in the sap, but are not in a form which can directly be made use of by the cells. In order that they may be rendered serviceable these bodies must be changed into more simple and diffusible forms. Thus both starch and inulin are polysaccharides $(C_6H_{10}O_5)_x$, and cane-sugar a disaccharide $(C_{12}H_{22}O_{11})$. To render them useful they must be changed into monosaccharides $(C_6H_{12}O_6)$ (cf. p. 139).

In the starchy seeds of all plants, and in their bulbs, tubers, or other reservoirs of reserve-materials, a ferment appears at or just before germination which is called diastase. Diastase is capable of transforming relatively enormous quantities of starch into glucose. It acts most powerfully at temperatures just below 70° C., but is very active at ordinary temperatures (15-20° C.). Although found most plentifully in these seeds and bulbs, it is present in smaller quantities throughout all parts of the plant. Baranetzky never failed to find it even in plants that abound in sugar, as the carrot and turnip.

Similarly, inulin in the tubers and root-stocks of the *Compositæ* is transformed into glucose, probably by a ferment of the same class, while cane-sugar is split into the monosaccharides, dextrose and lævulose, by invertin, a ferment identical with that formed by the glands of the intestinal mucous membrane in animals.

Cellulose, also, another polysaccharide formed from the assimilated starch, and the chief component of the cell-walls in plants, is converted into sugar in the germinating date-stone by means of another ferment. This ferment appears to be the active agent by which those fungi which live on the wood of trees transform cellulose into nutritive sugar.

A more particular study of the action of ferments on carbohydrates must be reserved until animal digestion is reached.

Proteids.—As starch is the first visible product of assimilation in plants, all other organic compounds contained in them must arise from or be built up upon it through chemical changes. The two elements which are absent in the starch molecule, but present in the proteid, sulphur and nitrogen, are, as we have seen, derived from the soil. That the formation of proteids from carbo-hydrate bodies with the addition of nitrogen and sulphur, through an inherent power of living protoplasm, is possible, follows from Pasteur's experiment on yeast. A few yeast-cells, fed with sugar and the salts mentioned, give rise to millions of new cells. Where the formation of the proteid molecules takes place is doubtful. The nitrates and sulphates absorbed by the roots penetrate to all parts of the plant, and may thus meet the carbo-hydrates transferred from the leaves in any part. The actual position has not been identified as yet. Some have suggested that the process may occur in the chlorophyll bodies themselves, perhaps during actual assimilation, perhaps during the night. Sachs, the greatest authority on this subject, suggests the sieve-tubes of the younger shoot-axes and leaves as the probable scene of the action. In them we find a proteinaceous slime, neither protoplasm nor organised proteid, but circulating proteid, evidently on its way to the younger growing organs. In their neighbourhood layers of cells may be seen filled with fine-grained transitory starch and with sugar, and other cells are often present in the immediate vicinity, in which calcium oxalate has crystallised out. Holzner long ago suggested that oxalic acid was formed in plants for the purpose of decomposing calcium sulphate, and thereby setting free the sulphuric acid for the production of proteid substances. It is possible, however, that the proteid molecule can be built up in any cell containing living protoplasm from another nitrogenous body, asparagin, which abounds in the sap of growing shoots and in stock reservoirs. Asparagin is an amide, amido-succinamic acid, $C_4H_8N_2O_3$, containing no sulphur. It is crystallisable and soluble in water, more readily in warm than in cold. Whether it is formed in the plant by synthesis, and converted into proteid by a like process and by the addition of sulphur, or whether it always arises from splitting up of proteid matter, is doubtful. Asparagin is certainly formed from proteids in many germinating seeds, to be re-converted into proteid again when the green organs begin to assimilate nitrogenous material, and if

asparagin arising in this way can unite with sulphur and undergo such molecular changes as are necessary to form proteid, it is exceedingly probable that it can be produced from the carbo-hydrates and salts for the same purpose. In addition to the proteids used up in the growth of plants, many species lay up in their reservoirs a store of reserve material. In most plants this store consists both of living protoplasm and of soluble non-organised proteid. In some plants a portion of the simple proteid, but always a relatively small part, may be present in the form of crystalloids. These remarkable bodies resemble true crystals in every particular save that they are capable of swelling by imbibition. The crystals in starchy seeds differ from those in fatty seeds. In the first they occur between the starch granules, in the second within the so-called aleurone grains. These consist of small masses of proteid substance in an amorphous state, and almost always contain a crystal of pure proteid. *Ricinus communis*, the castor oil plant, presents very fine examples of these bodies. Crystals of proteid bodies have also been found in other parts of plants apart from the reservoirs of store material, and are to be regarded as temporary deposits of nutriment for special purposes of metabolism.

Carbo-hydrates.—There can be no difficulty in assigning the production of the various carbo-hydrates which abound in plants to the results of chemical changes in the starch formed by the leaves. The different agents at work will be considered more particularly later.

Fats.—Fats play a very important part in the vegetable economy. All living protoplastic cells contain fat, while the great majority of ripe seeds contain large quantities, alone or together with starch. The manner in which they are formed from the starch assimilated by the chlorophyll bodies is chemically uncertain, but that they do arise in this way is proved by the fact that an unripe seed, as of *Pæonia*, which contains no fat but only starch, if detached from the plant and allowed to lie in moist air develops fatty oil, at the expense of its starch.

We have now found that the various carbo-hydrates, fats, and proteid bodies in the plant originate wholly or in part from the starch formed by the chlorophyll, and that the portions unused for active growth are stored up as reserve material. *The general principles underlying vegetable metabolism are construc-*

tive, in direct contrast to those of animal metabolism, which are, first, largely destructive; secondly, constructive.

In plants devoid of chlorophyll, or containing so little that it is scarcely of any importance, organic substances must be absorbed as such; they cannot be built up within. As there cannot be any assimilation of carbon from the carbonic acid gas in the air, this element must be absorbed in the form of carbonaceous compounds. Hence all plants devoid of chlorophyll are parasitic. They derive their nourishment from living plants or animals, or from the dead bodies of plants and animals, or their dissolved constituents. This use of prepared compounds is parallel to that in the seeds and young shoots of green plants before the chlorophyll has been developed, when they make use of pre-formed reserve materials. All parasitic plants, however, are not necessarily devoid of chlorophyll, as, for example, the mistletoe, but supplement the carbon obtained from the air with that drawn from their host. Similarly the carnivorous plants, which are more fully considered in the next chapter, supplement their scanty store of organic matter by the digestion of flies or from other nitrogenous foods.

Perhaps among the plants which do not possess chlorophyll the most important class is that of the *Fungi*. The distinguishing feature in the processes by which the fungi in general obtain their nourishment consists in the vast amount of apparently useless work performed. They obtain the compounds required from living and dead matter, but in the process they alter much of the medium on which they are living, often in a manner inimical to their own growth, and useless for their development. Thus yeast breaks up much more grape-sugar in the process of fermentation than is requisite for its nourishment, and some bacteria form so much lactic acid from sugar that their further growth is inhibited by it.

A still more peculiar method of nutrition pertains to the *Lichenes*. They are fungi which extract little organic nourishment from the trees or rocks on which they grow, probably no carbon, but some nitrogen and sulphur from the salts containing these elements. To make up for their lack of chlorophyll they weave themselves round and imprison small chlorophyll-bearing *Algæ*, and obtain from these the carbon required. These *Algæ* were formerly regarded as part of the

lichen itself, and were termed gonidia, but the true relationship between them has now been firmly established.

III.—COMPARATIVE DIGESTION IN PLANTS.

Bacteria, Schizomycetes—Yeasts, Saccharomycetes—Lichens and Fungi.—The various forms of *Bacteria* occupy the lowest position in the scale of organised matter. Although the majority of the species included under this title are of microscopic size (some, micrococci for instance, as minute as 0.2 micro-millimetres in diameter), each individual is capable of absorbing nutritive material and of transforming it, by appropriate means, into assimilable forms. It is one of the marvels of Nature that such infinitesimal specks of matter—0.2 micro-millimetre corresponds to 0.00006 inch, or $\frac{6}{100000}$ inch—should be able to carry out processes very similar to those in the higher animals. They are made up of a particle of protoplasm surrounded by a thin wall of a carbo-hydrate material closely allied to cellulose. The almost inconceivably small particle of protoplasm, the *mycoprotein* of Nencki, which forms the bacterium proper, is endowed with the power of secreting ferments, which act both intra- and extra-cellularly.

Many of the special properties which are distributed among different tissues in the individual higher forms are distributed in bacteria among different species. All bacteria, however, require the presence of nitrogen in an available form for their growth; they cannot make use of the free nitrogen of the air, but are able to extract it from ammonium salts, nitrates, proteid bodies, and, according to Nægeli, from such bodies as acetamide, methylamine, asparagin, and leucin. But while some can obtain all the nitrogen which they require from ammonium salts or nitrates, and do not make use of any proteid bodies present, others again obtain it by preference from these bodies.

As the fungi are unable to obtain carbon from the carbonic acid in the air, owing to their lack of chlorophyll, they must procure it in another way. Accordingly we find that they can extract carbon from various kinds of organic compounds. It is owing to this power of decomposing organic compounds, especially when these are of simple composition, that science has been enabled to gain a clear insight into their action in the acquirement of the requisite carbon. Thus Pasteur, in 1858, using ammonium tartrate, $(NH_4)_2C_4H_4O_6$, as a nutrient medium

in which to cultivate moulds, yeasts, and bacteria, found that they could obtain from it all the carbon and nitrogen they required.

Nægeli considers the nutritive solution suggested by Mayer in 1869 an excellent medium for yeasts. This solution was made up as follows :—

Water	100 c.cm.
Sugar	15 grms.
Ammonium nitrate	1 ,,
Acid potassium phosphate . . .	0.5 ,,
Tribasic calcium phosphate . . .	0.05 ,,
Magnesium sulphate	0.25 ,,

Theoretically, three to four grammes of new yeast can be produced from the constituents of the solution as described, but Nægeli found that only one gramme is actually formed. The cause of this incomplete use of the material is no doubt due partly to the formation by the growing yeast-cells of bodies in which the elements are so combined that the cells can make no use of them, leading to a withdrawal of some of the theoretical nourishment, and partly to the inhibiting action on the cells by these or other newly-formed bodies. As, however, a single yeast-cell weighs only about one two-millionth of a milligramme, or one two-thousand-millionth of a gramme, the formation of one gramme of yeast represents the development of 2000 millions of new cells composed of protoplasm and cellulose. This solution is only one of many which may be employed. In nature, glucose is the most suitable source of carbon available for the fungi.

Fungi are able to obtain nitrogen from certain substances, as from urea and oxamide, although they cannot make use of the carbon also present.

Fungi require, however, in addition to carbon, hydrogen, oxygen, nitrogen, and sulphur, the presence of mineral matter. All native proteids contain a small proportion of inorganic salts. When this is removed by artificial means the proteids lose some of their characteristic features (cf. p. 145). The protoplasm of fungi is no exception to this rule. Nægeli supposed that phosphorus, an element of the potassium-cæsium series, and one of the series calcium, barium, magnesium, or strontium, were sufficient. He thought that iron was unnecessary, and that they could grow if one of the elements, calcium

or magnesium, was available, unlike the higher plants for which both were required. Molisch lately (*Sitzungsber. der Kais. Akad. d. Wissenchaft*, Wien, 1894) has shown that Nægeli did not use sufficiently pure salts. Molisch purified all the salts used by several re-crystallisations. The results of his investigations show that after twenty days the growth of yeasts with iron sulphate is three times as great as the growth of yeasts cultivated under the same conditions but without the addition of iron. Neither manganese, cobalt, nor nickel have this effect, and cannot replace the iron. Molisch finds, also, that calcium cannot replace magnesium. Fungi grown in solutions containing calcium but no magnesium salts do not produce spores; nor can barium or strontium be substituted for magnesium. He concludes that while magnesium is absolutely essential for the proper development of fungi, calcium may be withheld without detriment to them; and that in this particular the fungi differ from the higher green plants.

The elements necessary, according to Molisch, are nine in number—

Carbon.	Nitrogen.	Phosphorus.
Hydrogen.	Sulphur.	Magnesium.
Oxygen.	Potassium.	Ferrum (Iron).

And in higher plants, Calcium (Lime).

The arrangement of the conditions appertaining to the supply of nutriment and to its absorption in the *lichenes* affords one of the few examples to be found in nature where a parasite and its host live together harmoniously and confer mutual obligations one on the other, even although the host exercises some degree of compulsion in the retention of the parasite.

Lichens belong to the subdivision *ascomycetes* of the *fungi*, but differ from other members of their subdivision in that they weave themselves round microscopic *algæ*, and imprison them in a thallus of densely interwoven hyphæ. Before the true structure of *algæ* was known the existence of two different forms of tissue had been detected—fungus tissue producing organs of fructification, and cells containing chlorophyll. These green bodies were termed gonidia.

Bornet and Stahl demonstrated that the union of the *fungus* and the *algæ* promoted the vigour of both. The *algæ* serve as organs of assimilation, in the same manner as chlorophyll cells

elsewhere, and the *fungus* obtains the inorganic constituents necessary for the growth of the combined individual.

It is for this reason that lichens are independent of organic soils. Other *fungi* must be supplied with organic material from which to abstract carbon and nitrogen. Lichens, thanks to the imprisoned *algæ*, can develop on rocks, even on crystalline rocks, from which they are able to obtain the mineral matter required for their own growth and for the proper nourishment of the chlorophyll cells represented by the captive *algæ*.

Owing to their independence of organic substrata the lichens have a much greater choice of sites whereon to establish themselves than any of the other fungi.

Higher Plants.—The general description which has already been given of the phenomena of vegetable metabolism applies to almost all of the higher members of the vegetable kingdom. Chlorophyll bodies present in their leaves or analogous structures decompose the carbonic dioxide[1] in the air under the influence of sunlight and heat, and build up more stable compounds containing a greater proportion of carbon and less oxygen for the nourishment of the plants. In the dark this process of assimilation ceases, carbonic dioxide is given off and oxygen absorbed. In the daytime the roots and leaves absorb carbonic dioxide, the oxygen of which is set free by the chlorophyll of the leaves; during the night the roots may still absorb carbonic dioxide, but it is exhaled unaltered from the leaf surfaces. A part of the carbonic acid gas exhaled in the hours of darkness may arise from oxidation of carbon by some of the oxygen absorbed.

The first leaves of the higher plants to emerge from the seed are usually fleshy and more solid in appearance than those which appear at a later date. These cotyledons, or store-leaves, contain reserve nutriment which can be made use of by the growing plant at a time when the roots are insufficient to provide it with enough food. When a plant is capable of procuring sufficient nourishment through its roots and leaves the cotyledons atrophy.

Many plants lay up stores of aliment in the form of tubers, bulbs, and fruits for the use of the seeds when germinating.

[1] Carbonic dioxide, or carbonic acid, is formed by two atoms of oxygen and one atom of carbon; it is represented by the chemical formula CO_2.

An annual plant, flowering, seeding, and dying in the space of a few months, grows quickly, provides little store of nutriment for its seeds, and after fructification commences to decay. The seeds contain some supply of food against their germination, develop chlorophyll-containing cotyledons of a proportionately large size, and rapidly produce roots capable of supporting them. Biennial plants lay up a store of food material during the first year of life towards the accomplishment of maturation in the following year. The drain on the organism occasioned by the production of flowers and seeds is then too great for continued vitality. Perennial plants may be herbaceous, like the daisy and primrose, which when grown from seed germinate in one season, and in addition produce an underground stem or rhizome, from which annual flowering shoots are sent up. Other perennial herbaceous plants produce one shoot, which may flourish for years before flowering, after which decay sets in. Woody perennials may grow for a large number of years, their growth ceasing during the winter months. The annual drain upon their vitality arising from the process of flowering and fructification has so little effect on their power of development, that they continue to produce flowers and fruit each year throughout their life. Some perennial plants retain their leaves unaltered throughout the annual resting period, only shedding them when a fresh crop is ready to take their place, thus receiving the name of evergreens.

To summarise the main facts connected with vegetable nutrition, leaving out of account the carnivorous plants, which are fully discussed in the next chapter, we may state that—

A. Plants obtain—

i. Their carbon by decomposing carbon dioxide. Some plants possibly can absorb organic compounds containing carbon, such as are present in decaying vegetable or animal matters in the form of organic acids.

ii. Nitrogen from the nitrates and ammonium compounds in the soil. A few plants may be able to absorb nitrogen from the nitric acid present in rain water caught in hollows or receptacles in their structure.

iii. Hydrogen and oxygen from water.

iv. Mineral salts from the soil by means of their root-hairs.

B. Plants elaborate carbo-hydrate bodies from the carbon separated from carbon dioxide, and the hydrogen and oxygen in water; proteids from the nitrogen obtained by the roots and the already formed carbo-hydrates, probably through protoplasmic action; and fats from the carbo-hydrates.

C. Part of the elaborated material is used up at once, and part is stored up as a reserve stock in the fruit or seed to serve for its nourishment during germination; and in most cases in different parts of the plant itself, this store being formed in summer and made use of during ordinary growth, but especially in springtime during budding.

D. Plants produce the complex bodies which go to form their various organs and secretions from simple elements.

E. They are constantly absorbing water from the soil and giving it off again into the air from their leaf surfaces. These surfaces, however, are generally supplied with stomata (cellular valves) whereby this transpiration may be regulated.

F. Plants possess no true circulatory apparatus. The movements of the sap are chiefly produced by diffusion and follow the laws of osmosis. The actual causes originating osmotic action arise from the exhalation of water, elastic pressure of the cell walls, movement of the branches, alterations in temperature, and the abstraction of water in the elaboration of chemical compounds. Capillary attraction has also some effect on the movement of the sap.

G. Numerous bodies, included in the class of unorganised ferments, are present in many plants, by whose agency alterations in the complex substances formed in the first instance from simple elements are brought about, whereby they are rendered more readily available for purposes of nutrition.

H. In plants the organism is protected from the growth of harmful agents by the circulation and acidity of its juices; in the animal organism secondary defensive means are supplied by the presence of phagocytes, and by reason of the existence of a nervous system capable of initiating actions tending to the avoidance of danger.

CHAPTER III.

CARNIVOROUS PLANTS.

CARNIVOROUS PLANTS WITH ADHESIVE APPARATUS—*Drosophyllum lusitanicum.*

CARNIVOROUS PLANTS WHICH SHOW MOVEMENTS IN THE CAPTURE OF THEIR PREY—*Pinguicula vulgaris*—Structure—Digestion—*Drosera rotundifolia*—Structure—Inflection of Tentacles—Aggregation of Protoplasm—Digestion and Absorption—Digestive Power on Different Substances—*Dionæa muscipula*—Description—Mechanism—Sensitive Hairs—*Aldrovanda vesiculosa.*

CARNIVOROUS PLANTS WITH TRAPS FOR THE CAPTURE OF INSECTS—*Nepenthaceæ*—Pitchers—Secretion—*Cephalotus follicularis*—*Lathræa squamaria*—*Bartsia Alpina*—*Utricularia neglecta*—Insects not truly digested by it—*Genlisea ornata*—*Heliamphora nutans*—*Sarracenia purpurea*—Summary—Authorities.

ONE of the most wonderful things in Nature is the development by some genera of the vegetable kingdom of the power of supplementing their nitrogenous intake by the digestion or dissolution of animal bodies. The number of plants which are capable of preparing and assimilating proteids may be estimated at about five hundred. As insects form their staple diet, they have been termed "insectivorous plants"; the names of "flesh-eating" or "flesh-consuming" have also been applied to them. Since, however, the chief and most important part of the process lies in the utilisation of the albumins in the flesh of the prey, the term "carnivorous" is more properly applicable. But even this term does not cover the whole question, for many carnivorous plants extract the proteids from pollen and seeds as readily as from unwary insects.

Carnivorous plants can live without the extra supply of nutriment derived from captured prey, but they thrive better, grow larger, and are more fruitful if chances of procuring proteids from animal bodies be afforded them. It is one of

the most difficult questions in connection with the theory of the origin of species to explain satisfactorily how plants have developed such carnivorous tendencies. The first point to note is, that almost all the species live in soil poor in nitrogenous compounds; secondly, that the work done by very complicated mechanisms appears to be quite incommensurate with the results achieved. It is known that the seedlings of all conifers, monocotyledons, and those dicotyledons which are provided with endosperm, are able to absorb organic and nutritive substances through their leaves. The wonderful thing about the carnivorous plants, then, is not the fact of their being able to absorb nourishment from organic compounds, but the marvellous adaptations of simple organs developed by nature for the purpose. Argument, however, along the lines of "the survival of the fittest," will show that plants, growing in soil poor in nitrogen, must thrive best if an extraneous supply of that element be afforded them, and a process of modification of existing organs to that end, through countless ages, has led to an extraordinary development of what at first were doubtless simple contrivances. Nothing stands still in nature, and reckoning by the faint records of the dim and distant past as seen in connection with other modifications of structure, slight changes which might serve the purpose of capturing a stray insect may in the course of time be specialised into the complicated arrangements which now excite our wonder and admiration. In highly specialised organs, Nature, working under no agreement as to time, is seldom a niggardly contractor.

As the number of carnivorous plants is so large it is necessary to divide them into classes for the purpose of description. The first class comprises those plants which are provided with leaves covered with an adhesive substance to which the insects stick, but which exhibit no movements whereby the prey may be held fast. The second group consists of plants which exhibit movements in the capture of their prey, while they secrete, in addition, a sticky fluid which serves in the first place to entangle and then digest the prisoner. The third class of carnivorous plants possesses traps or pitfalls contrived in their substance, which serve to entrap insects. This class may be subdivided into two groups. In the first the captured insects are not digested but decay, and the products of decay are absorbed; in the second a

digestive fluid is secreted which serves to simplify the organic compounds contained in the bodies of the insects, and render them more easily assimilable.

CLASS I.—CARNIVOROUS PLANTS WITH ADHESIVE APPARATUS.

The leaves of the plants in this class act like lime-twigs, their surface being studded with glandular cells which secrete a sticky fluid to capture their prey, and juices to digest it when caught. They can also re-absorb these juices along with the proteids dissolved in them. The best known member of this group is the Fly-catcher (*Drosophyllum lusitanicum*) of the order *Droseraceæ*. This plant lives in Portugal and Morocco, and, unlike the majority of carnivorous plants, is found in dry, sandy, or rocky soil. The stem is about nine inches in height, and bears at the top a few short branches crowned with flowers from 2 to 3 cm. in diameter. The numerous leaves spring from the stem close to its base, and are long, slender, and filiform, the upper surface being slightly grooved to form a narrow channel. Both surfaces of the leaves, with the exception of the channel, are covered with small glands, shaped like mushrooms, which glisten in the sun like dewdrops owing to the drop of secretion on the summit of each. These glands are supported on pedicels, and are arranged in irregular, longitudinal rows. They differ much in size and shape, in the height of the pedicels, and in their colour; some may be purple, some a bright pink. In shape the glands resemble those of the *Pinguicula* (cf. p. 47), in colour the tentacles of the *Drosera*, while the drop of colourless fluid covering the top of the gland corresponds to the similar secretion seen in *Drosera*. The pedicels contain spiral vessels, connected below with the fibro-vascular or circulatory system of the leaves, and above with cells in the glands themselves, which are marked with fine spiral ridges. The spiral cells of the glands usually number from eight to ten, and are covered by two layers of delicate angular cells. Similar glands are also to be found on the flower stalks and calices. In addition to these pedunculated glands there are numerous sessile, colourless glands smaller in size, which differ from the stalked in that they only secrete fluid after stimulation with albuminoid material. The secretion of the larger glands is very acid, even before excitation; that of the sessile glands is

also acid; both are viscid. The glands of either kind have the power of rapidly absorbing nitrogenous matter. The drops of secretion are readily removed from the glands. Owing to this circumstance an insect alighting on a leaf of *Drosophyllum* soon gets clogged by the viscid secretion adhering to its wings or legs; crawling on, as it is unable to fly, it is soon bathed in the fluid, and sinking down on the sessile glands, dies suffocated.

The glands replace the drops of secretion removed from their surface with great rapidity, and can secrete large quantities of acid juice. It is not an uncommon thing to see a plant covered with dead insects, exhausted of their nutriment, and at the same time with numbers of struggling captives which have recently alighted. Darwin noticed that, although the glands absorbed their secretion in about an hour and a half if a proteid or a drop of nitrate of ammonia were placed upon them, no such absorption could be detected when small bits of glass or charcoal were used in the same way. That is to say that nitrogenous bodies have some special action on the protoplasm of the gland-cells leading to the rapid absorption of their secretion with its contained nitrogenous material. In connection with this absorption of nitrogen a marked change in the protoplasm of the cells which compose the glands occurs. This change is termed "aggregation," and will be more fully dealt with in treating of the digestive processes in *Drosera*. Aggregation of protoplasm causes the cells to take on a much darker hue, and is probably due to the processes necessary for the secretion of the acid used in the digestion of the proteids of their prey. That this is the probable reason is shown by the fact that, while carbonate of ammonia, if placed on the glands, primarily causes a darkening of the cells, cells which have been fed on meat infusion lose their deepened colour on the subsequent application of the same salt in solution. In the first case the application of the solution of the ammonia salt causes secretion of acid which neutralises it; in the second, the contents of the glands which have already secreted acid, part of which has probably been used up in digestion of the meat infusion, are rendered neutral or alkaline with destruction of the colouring matter. The *Drosophyllum*, unlike many of the other carnivorous plants, does not secrete very much more fluid after stimulation by albuminous substances than before, but the fluid becomes more acid and contains more ferment.

Owing to the fact that it is already acid before stimulation the secretion of the *Drosophyllum* digests animal matter more quickly than the *Drosera*. The glands absorb the results sooner and begin to secrete fluid again in a much shorter time. The sessile glands appear to have more power of digestion than those furnished with stalks; the latter serve chiefly to entangle the insects.

Among the other plants which capture insects by means of an immobile adhesive apparatus I may mention *Roridula dentata*, a native of the Cape of Good Hope, and similar in many respects to *Drosophyllum; Byblis gigantea* (Western Australia); *Sedum villosum;* and many members of *Primula*, *Saxifraga*, and *Sempervivum.*

CLASS II.—CARNIVOROUS PLANTS WHICH SHOW MOVEMENTS IN THE CAPTURE OF THEIR PREY.

The genus *Pinguicula*, of which nearly forty species are known, several members of the genus *Drosera*, the *Dionæa muscipula*, and some species of the *Aldrovanda vesiculosa* may be included in this class. They will be discussed in the order in which they are placed, which is based on the complexity of the arrangements for the capture and digestion of insects.

Pinguicula vulgaris.—This plant is an inhabitant of damp and boggy places on moors, commons, or mountains. The area of its distribution covers the whole of the arctic and sub-arctic regions of the globe, and stretches down as far south as the Baikal Mountains, the Balkans, and the Pyrenees, generally along the mountain ranges. The plant is in the form of a rosette, eight to ten leaves branching out from the centre, and lying flat on the ground with their under surfaces touching it. The leaves are oblong-ovate, yellowish-green in colour, with scarcely any footstalk, and with their edges slightly upturned and incurved, converting the surface of the leaves into shallow troughs. (See Fig. 2.) The upper surface is studded with numerous glands which are of two kinds, one, the larger and visible to the naked eye, is supported on a unicellular pedicel, the other variety is smaller and practically sessile. A square centimetre is said to contain 25,000 glands, and a rosette of six or eight leaves to bear about half a million of them. All the glands secrete a viscous, colourless, and neutral fluid. The larger stalked glands secrete this fluid in greater quantity than those which are sessile. The stalked glands, which very closely resemble a mushroom when examined under the

microscope, appear circular from above, the cap being divided into ten or sixteen cells by radiating partitions. These cells are filled with a pale green, homogeneous fluid. The pedicel is composed of one elongated cell, with a nucleus and nucleolus resting on a slight prominence of the leaf's surface. Towards the base of the leaf, and especially near the midrib, these glands are supported by multicellular pedicels, while the cap is smaller. The smaller glands differ only in being composed of about half the number of cells, the fluid of which is much paler. They are also supported on slight elevations of the leaf surface. Ordinary flat epidermal cells fill up the spaces between the glands, with occasionally the guard-cells of stomata. The writer has found small sessile glands, composed

FIG. 2.

THE COMMON BUTTERWORT (*Pinguicula vulgaris*).

(From a pen-and-ink sketch by the Author.)

Cross section of a leaf (× 20) of *Pinguicula vulgaris*. *A*. Vessels of midrib. *B*. Stalked glands. *C*. Shortly stalked glands. *D*. Sessile glands on dorsum of leaf. *E*. Incurved edge of leaf over an insect allowing a greater number of glands to come in contact with the prey.

of only four cells, on the under surface of the leaf, but they are so few in number that it is impossible to ascertain if they are capable of secreting digestive juices. The under surface, in addition, is thickly studded with stomata. The leaves are richly provided with fibro-vascular systems. The spiral vessels, proceeding from the midrib, terminate in cells marked by a spiral line close to the edge of the leaf. The flower is of a violet-blue colour, with petals covered with long velvety hairs, and with a spur at the back. It is borne on a long, slender, gracefully curved stalk, which rises from the centre of the rosette of leaves. The roots are short, seldom exceeding 1.5 inch.

The leaves, when looked at with the naked eye, present a

large number of minute shining points, especially if a light be thrown on them at an angle towards the observer. Under a magnifying-glass these shining points produce a remarkably pretty effect, and are then seen to be due to the drops of secretion surmounting each of the glands. When an insect alights on a leaf it is at once held fast, if it be small enough, by these drops of viscid fluid. In like manner grains of pollen, minute plants, and seeds are frequently found attached to the leaves. Darwin examined a large number of wild plants, and found that about 70 per cent. had captured insects, while many had caught various small seeds as well. Shortly after the capture of an insect the glands in contact with it begin to secrete a larger quantity of fluid, which is still more viscous than that exuded in the fasting condition, and which is strongly acid in reaction, the previous secretion having been neutral. In a few hours the edges of the leaf begin to curve in towards the spot where the insect lies, and the glands directly in contact pour out so much fluid that the prey is submerged in it. Although the presence of any nitrogenous particle is sufficient to cause incurvation of the edges of the leaf some distance, it may be, from its actual position, none of the glands except those in direct contact secrete the digestive fluid. If the insect be caught on one side of the leaf, that side alone exhibits any movement. If, however, its position is close to or on the midrib, both edges curve in over it. The apex of the leaf never moves towards the base. The glands themselves have no power of movement. A remarkable fact with regard to the incurvation of the leaves is the comparatively short time which it lasts. Darwin found that in no case was there any marked incurvation before 2 hrs. 17 mins.; after drops of raw meat infusion had been placed on the leaves he thought he could detect traces of movement in 1 hr. or 1 hr. 30 mins. As a rule, well-marked re-expansion occurred within twenty-four hours, and always before forty-eight hours had elapsed. Reference to Table II., which has been compiled from Darwin's observations, will show the different periods at which incurvation of the edges of the leaves, and the secretion from the glands, began and ended. Darwin also pointed out that though fragments of glass caused a certain degree of incurvation, which began as soon as that following stimulation with proteid bodies, it lasted a much shorter time, and was not accompanied by any secretion. A leaf that has become well

incurved and has again expanded does not respond to a fresh stimulus for a considerable time.

TABLE II.—*Facts regarding the Secretion of the Glands and the Movement of the Edges of the Leaves of the Pinguicula Vulgaris after stimulation with various substances.* (*Compiled from Darwin.*)

Substances placed on Leaves.	Position.	Secretion.			Movement of Leaves.		
		Re-action.	Be-ginning.	Leaves Dry.	Be-ginning.	Height of Move-ment.	Un-curved.
Small Flies........	Margin.	Acid.	—	4 days	—	15 hours	—
Fragment of Large Fly	Near Apex.	Acid.	—	4 days	4 h. 20 m.	—	48 hours
Do.	Medial line.	Acid.	—	—	3 hours (both edges).	4 h. 20 m.	—
Roast Meat	Margin.	Acid.	40 mins.	1 to 6 dys	—	24 hours	48 hours
Meat Infusion on Sponge	Margin.	Acid.	—	—	2 h. 17 m.	6 h. 30 m.	3 days
Infusion of Raw Meat	Margin.	Acid.	At once	3 h. 20 m	2 h. 17 m.	7 hours	24 hours
Do.	Medial line.	Acid.	At once	3 h. 20 m.	3 h. 27 m.	10 hrs. 37 mins.	24 hours 20 mins.
Carbonate of Ammonia in Solution (1 gr. to 2 oz.) ..	Margin.	?	At once	?	1 hour.	3 h. 30 m.	24 hours
Fragments of Glass	Margin.	Neutral	None.	None.	2 h. 30 m. (very slight).	2 h. 30 m.	16 hours 30 mins.
Cabbage Seeds....	Margin.	Acid.	4 hrs. 30 mins.	Several days.	2 h. 25m.	20 hours	48 hours

Scratching surface with blunt needle, no effect.

The incurvation of the leaves in the *Pinguicula* appears to serve three purposes: to prevent the prey from being washed away by rain before digestion, to oppose a greater secreting surface to the captured animal, and to gradually push any larger object than usual, over which the edge is not able to reach, towards the centre of the leaf, by which means it is brought into contact with a far greater number of glands than would be the case if it remained in one spot.

It is a curious fact that the simpler forms of proteid—for instance, albumoses—although they cause secretion of an active juice, have little power of producing a marked incurving of the leaves. The author made a number of experiments with different forms of proteids, the main results of which are summarised in the following tables.

As the incurvation after stimulation with egg-albumin and serum-globulin exactly corresponded to that recorded in Darwin's work, no further notice of it need be taken. When small quantities, about 3 m.gr., of proto-albumose, deutero-albumose, or pure peptone were placed on the leaves, little if any movement of the edges took place.

It will be seen from the table (Table III.), that of the proteids employed serum-globulin, separated and used in a dry state, and blood fibrin, stained with carmine and dried, excited no secretion. Of the others, proto-albumose caused the greatest flow, while peptone (Table IV.) dissolved almost at once in the secretion already on the glands, excited very little further secretion, was absorbed within twenty-four hours, and killed the part of the leaf on which it was placed in a short time. A solution of raw egg-albumin mixed with alum-carmine and boiled allowed of very small portions of the proteid impregnated with the stain being placed on the leaves. The albumin was absorbed in time, but not so quickly as when unstained, while specimens of the leaves examined under the microscope after mounting in Canada-balsam gave evidence of the absorption of some of the carmine, at any rate by the glands.

TABLE III.—*The Time taken by the Leaves of the Pinguicula Vulgaris to Dissolve and Absorb different Proteids.*

Proteid Given. April 12th, 8 p.m.	Apr. 13th, 9 a.m.	Apr. 13th, 2 p.m.	Apr. 14th, 9 a.m.	Apr. 15th, 6 p.m.	Apr. 15th, 6 p.m.	Apr. 16th, 9 a.m.
Raw Egg Albumin	Dissolved, small drop.	Mostly absorbed.	Dry.	—	—	—
Proto-Albumose	Dissolved, large drop.	Drop smaller.	As before.	Small drop, brown.	Smaller.	Dry.
Deutero-Albumose	Do.	No change.	Partly absorbed.	Large drop, no colour.	As before.	As before.
Pure Peptone ..	Partly absorbed.	Absorbed, leaf wrinkled, dry.	Leaf dying.	As before.	As before.	As before.
Serum Globulin	Not dissolved, no secretion.	No change.	Slightly moist, a little less.	As in last.	As in last.	As in last.
Blood Fibrin stained with Carmine ..	Dry, no change.	No action.	No action.	No action.	No action.	No action.
Coagulated Egg Albumin coloured with Carmine	Moist round patches of red.	As before.	Drier.	As before.	Albumin absorbed, Carmine left.	Dry.

Table IV.—*The Absorption of Peptone.*

A small quantity of pure peptone in powder placed on leaf at 6 P.M.

6.5 P.M.—All dissolved, forming a yellow solution in small drops.

6.7 P.M.—A few brown drops, a little larger.

6.14 P.M.—Drops paler again, fewer, some coalescing.

6.19 P.M.—No incurvation of edges, drops running more together.

8 P.M.—No incurvation of edges, one large pale drop.

9 A.M. (next day).—All absorbed, leaf dry and wrinkled.

1 P.M. (next day).—Leaf dry, becoming discoloured where peptone had been placed, healthy in rest of leaf.

Forty-eight hours from the beginning the portion of leaf on which the peptone had been placed was dead; it was yellow, dry, and sharply separated from the surrounding healthy portions.

For the purpose of investigating the rate of growth of plants fed on different proteid substances, I selected fourteen plants and placed them under identical conditions. The greatest breadth of each was measured from tip to tip of the longest leaves. Once a week they were fed with the substances enumerated in the table (Table V.), two individuals with each variety, and each week they were carefully measured. The two plants which received nothing grew to a little more than double their original size in four weeks; their increase was 109.4 per cent. The only other plants which exceeded this rate of growth were those fed with proto-albumose, in whom the increase amounted to 120.6 per cent. It will be seen that peptone had actually a retarding effect.

Table V.—*Showing the Results of Feeding Pinguicula Vulgaris with various Proteids.*

Proteid given each Week (Beginning April 12th, at 8 p.m.).	Growth in Inches (Greatest breadth from tip to tip of leaves).						
	April 12th.	April 19th.	April 26th.	May 5th.	May 10th.	Per Cent. of Growth.	
Nothing	1.75	1.87	2.62	3.00	3.25	85.6	109.4
Do.	0.75	0.87	1.37	1.75	1.75	133.3	
Raw Egg Albumin ..	1.37	1.62	2.12	2.25	2.25	64.2	57.1
Do.	0.75	1.00	1.25	1.50	1.50	50.0	
Proto-Albumose	1.50	1.87	2.62	3.00	3.12	108.0	120.6
Do.	0.75	0.87	1.37	1.75	1.75	133.3	
Deutero-Albumose ..	1.25	1.62	2.00	2.50	2.50	50.0	62.5
Do.	1.00	1.37	1.50	1.75	1.75	75.0	
Pure Peptone	1.12	1.25	1.50	1.87	1.75	56.2	42.6
Do.	1.06	1.12	1.50	1.62	1.37	29.2	
Serum Globulin	1.25	1.50	1.75	2.00	2.00	60.0	80.5
Do.	0.87	1.00	1.12	1.50	1.75	101.1	
Coagulated Egg Albumin stained with Carmine ..	1.25	1.50	2.12	2.25	2.50	100.0	84.8
Coagulated Egg Albumin stained with Carmine ..	1.62	1.75	2.25	2.62	2.75	69.7	

The secretion of the glands is neutral in the fasting state, but shortly after direct stimulation with a nitrogenous body becomes acid and contains a ferment with an action similar to that of pepsin. The acid belongs to the acetic acid series, and is probably either acetic acid or formic acid. The secretion acts on proteids in the same way as the gastric secretion of animals, while the glands absorb the products of digestion, leaving the insoluble matter on the leaf. After absorption the glands dry up, and the indigestible material left is blown away by the wind or washed off by the rain. The protoplasm of the cells in the glands exhibits all the phenomena of aggregation which can be seen so well in *Drosera*, and will be further described under that plant. *Pinguicula* probably secretes another ferment in addition to the pepsin. Linnæus one hundred and fifty years ago mentioned that the Laplanders had a very favourite dish, similar to our junket, called "Tätmiölk." This is made by pouring milk, warm from the cow, over butterwort leaves, when a peculiar tough mass of a cheesy consistency is formed. This may be partly due to the acid secreted, partly to a rennet ferment. The secretion is also strongly antiseptic, and here again popular empiricism foreshadowed scientific discovery, for the shepherds in the Alps have long used the leaves as a cure for sores on the udders of their cows, the virtue lying in their antiseptic action.

Two other specimens of *Pinguicula*, *P. grandiflora* and *P. lusitanica*, behave in the same way. *P. lusitanica* has naturally much incurved leaf-edges, but they become very strongly inflected over organic bodies, to a greater degree than in *P. vulgaris*, and remain incurved for a longer time. *P. grandiflora* is more easily managed under cultivation than *P. vulgaris*, and is therefore more suitable for experimentation.

The members of the genus Sun-dew (*Drosera*) have the same habitats as *Pinguiculæ*, and are usually rooted in the boggy, dark soil of moors. The *Drosera rotundifolia* is commonly found on the moors of this country, and will be particularly described. As in the *Pinguicula*, and indeed in many other carnivorous plants, the leaves of the *Drosera* form a rosette with their lower surfaces adpressed closely to the ground and grouped radially round a slender flower-stalk. The leaves are peculiar and characteristic. Circular in shape, numerous filaments or tentacles of a delicate claret colour stand out from their upper surface. Each tentacle carries at its free end a terminal gland which, when the leaf is healthy, is surrounded by a glistening drop of fluid, from which the name of sun-dew is derived.

Examination of one of the leaves with a lens shows that the filaments project from the upper surface and margin like pins from a pin-cushion, while they are seen to be of different lengths. Although there is a gradual increase in their size from the centre outwards we may separate them into three divisions: (1) Short perpendicular tentacles rising from the centre of the

leaf; (2) longer tentacles slightly inclined outwards, arranged round the last; (3) long, slender marginal tentacles springing from the edge of the leaf and directed outwards. The glands which surmount the central and intermediate tentacles are clavate, those of the long marginal tentacles are inserted on the upper surface of the free extremity, and are much more elongated; a good idea may be gained of their appearance if they be likened to a somewhat elongated hair-brush, the bristles being replaced by a pad. All the glands secrete a sticky, viscid fluid, which, especially after stimulation, may be drawn out into long threads (cf. Fig. 7).

There are also numbers of small sessile glands on the upper surface of the leaf, and some on the lower parts of the larger tentacles, composed of two or four cells, which stain much more deeply when the leaf is digesting than when it is fasting. The lower surface of the leaf is bare. Both surfaces show the guard-cells of stomata.

The secretion of the glands is neutral before stimulation, but if non-nitrogenous substances be placed in contact with it the quantity is augmented and it may become acid, but contains no ferment. If, however, an insect alight on the leaf, or a particle of a nitrogenous substance be placed on it, the secretion of the glands is poured out more freely and possesses active digestive properties. The ferment has the same action on proteid bodies as pepsin, and may be practically regarded as similar to that ferment. As in *Pinguicula*, the insect, soon after alighting on the leaf, becomes entangled and drowned in the fluid secretion of the glands; but there are two remarkable differences between the plants. In *Drosera* the tentacles respond to stimulation with all kinds of bodies, and the glands not directly in contact with them secrete more vigorously. The marginal tentacles exhibit the movements most conspicuously. If a small fly or a particle of albumin be placed on the gland of one of these tentacles, in a few seconds the tentacle may be seen to bend inwards, the movement commencing close to the gland. In from two to three minutes it describes an angle of 45°, and in ten minutes an angle of 90°. The most acute bend in its length is situated not far from the base. By this action the fly or albumin is brought into contact with the glands of some of the short central tentacles, and a greater power of digestion is thus obtained. But the response to stimulation goes further than this, for in about ten

LEAF OF DROSERA ROTUNDIFOLIA FED WITH PROTEID.

FIG. 3.

Photo, A. L. G.] [*Copyright.*

Leaf of *Drosera* (five times the natural size) before feeding.

FIG. 4.

Photo, A. L. G.] [*Copyright.*

Leaf of *Drosera* five minutes after a small piece of dry proto-albumose had been placed on it.

The dark mass to the right of the leaf represents the piece of proto-albumose, and just above and a little to the right of it the marginal tentacles can already be seen to have bent inwards.

LEAF OF DROSERA ROTUNDIFOLIA FED WITH PROTEID.

FIG. 5.

Photo, A. L. G.] [*Copyright.*

Leaf of *Drosera* twenty-eight minutes after feeding. The marginal tentacles over a large section of its circumference have bent inwards, and are shown foreshortened in the photograph. The whole surface of the leaf is darker, the stalk is also darker, while the proto-albumose has been largely dissolved and has spread out over a greater area.

FIG. 6.

Photo, A. L. G.] [*Copyright.*

The same leaf twenty-eight hours after feeding. The whole leaf and stalk dark, and apparently of smaller size owing to incurvation of leaf-edges. Many tentacles bent in upon surface, others out of focus before were brought into focus from change in shape of leaf. The five white marks over the upper part of the leaf are caused by light reflected from incurved tentacles. Many of the glands of the marginal tentacles are surrounded by drops of secretion.

minutes the tentacles in the immediate proximity of the first commence to bend in likewise, in another ten minutes tentacles further off follow suit, and in two or three hours all the tentacles may have converged on the prey (Figs. 3 to 6). As a rule the whole leaf becomes concave when all the tentacles have converged, and resembles a closed fist, and if the stimulation be strong enough, even the leaf and leaf-stalk may become more perpendicular. If more than one fly alights on the leaf the tentacles divide into sections; for instance, if one alights on one side, the other on the opposite side of the leaf, half the tentacles devote their attention to the one, the other half to the second. In fact the tentacles exhibit a combined action by which the greatest possible quantity of digestive secretion is brought in contact with the prey under all circumstances. The period during which the tentacles remain inflected depends on the size of the body captured. If very small two days suffice for the digestion and absorption of its nutritive constituents, if larger they may remain inflected for many days. Other circumstances, such as the age of the leaf and the temperature of the air, affect the length of time of inflection, but not nearly so strongly as the size and nature of the substance caught. I have seen a perfectly healthy leaf still tightly folded over a small portion of proto-albumose ten days after feeding it. The sensitiveness of the leaves is entirely confined to the glands and cells closely adjacent. The motor impulse passes down through the cellular tissue (not along the fibro-vascular bundles) to the lower part of the tentacles, which alone is capable of inflection. When the stimulation proceeds from the terminal gland, the tentacle always moves towards the centre of the leaf, but if it proceed from the shorter tentacles on the disc of the leaf, the direction of inflection of the marginal tentacles is towards the point stimulated. If a plant be immersed in a solution of a proteid, all the tentacles, save the short ones on the disc, move towards the centre. If a particle of a proteid substance be placed on the disc, the surrounding short tentacles bend in towards it as well as the longer ones. The motor impulse proceeding from one tentacle to another enters by the base, and causes inflection at once, a further impulse being sent up to the terminal gland. A reflex impulse, though unconnected with any nervous action, now proceeds down the tentacle, causing the protoplasm of the cells to aggregate into masses. That the centrifugal impulse extends to the glands is

shown by their increased secretion, which also becomes acid. The actual cause of the movement of the tentacles is obscure, but may be due to the contraction of the walls of the cells on the inner aspect during the process of aggregation. That these cells are in a state of contraction of some sort is shown by the fact that if the outer cells be shaved off during the inflection of a tentacle, the inflection is carried further until a complete circle is formed. Re-expansion, in like manner, is probably brought about by the normal elasticity of the outer cells, which is sufficiently active to cause the tentacle to rise up when the stimulus leading to the contraction of the inner cells is withdrawn. Ziegler advanced the theory that the motor impulses were conducted by the fibro-vascular bundles, but Darwin showed this to be erroneous by dividing the main bundles of several leaves without materially influencing the movements of the tentacles. We are forced, then, to conclude that the impulse passes through the cells, and depends on the irritability of the protoplasm in them. The impulse may be of the nature of a slight chemical change, or merely be occasioned by increased movement of the protoplasm. The fact that a stronger stimulus increases the rate of the impulse, and that the process of aggregation of the protoplasm, which follows the movement, can be observed spreading down the tentacles from cell to cell with a pause between each, makes it probable that another form of protoplasmic activity is the agent at work. It is propagated faster and has no power of itself to initiate aggregation, but like an efferent nerve-impulse, stimulates the glands, causing the requisite excitation of their cells for the transmission of afferent impulses to the cells involved.

Aggregation of Protoplasm.—Stimulation of the tentacles by any of the methods described above as capable of inducing movement in them also excites changes in the protoplasm of the cells of which they are composed. If the cells of one of the terminal glands be examined immediately after stimulation the contents can be seen to become cloudy, even in so short a time as ten seconds. Within a minute granules appear in the cells of the tentacles immediately below the glands, and these soon aggregate into larger masses, which show incessant changes of form. These masses consist of aggregated protoplasm. The stalk of each tentacle is penetrated by one or two vessels with delicate spiral markings on the inner surface, and around these are the parenchymatous cells. The gland

has in the middle several cells with similar spiral markings with which the vessels of the stalk communicate. Grouped round these cells are two or three layers of parenchymatous cells, in which the protoplasm can be discerned streaming round close to the walls; whilst in the centre there is a vacuole filled with a red-violet fluid. The phenomena known as "aggregation of protoplasm" occurs in the parenchyma, the contents of each cell dividing into a dark red-purple mass, as described above, and a clear colourless fluid. This change may be regarded as an expression of the activity of the cells, but does not depend on absorption, as it may be excited by a few touches; as a rule it is synchronous with the inflection of the tentacles, appearing just before the commencement of movement, and ceasing with full re-expansion. The process begins in the parenchyma of the glands and spreads down the cells of the pedicels; its progress is appreciably checked at the point of junction of the cells. If the stimulus applied to the gland be very powerful, all the cells down to the root of the tentacle may be affected. If the stimulus be applied to the short central tentacles the process of aggregation in the longer tentacles commences in the gland and travels down to the base. The active impulse communicated to the gland must, therefore, be different from the exciting influence generated by the gland itself. What this influence consists of is as yet unknown. It may be of the nature of molecular change transmitted from cell to cell, or it may be carried by the spiral vessels. It is a strange thing that a lowly vegetable, *sans* muscles, *sans* nerves, *sans* everything necessary to animal life, should be able to capture animals, and unerringly to direct its tentacles to one spot by means which apparently must be purely chemico-physical.

The author has found that the best method by which to obtain permanent records of the process of aggregation is to place an entire plant in a weak solution of a proteid, coloured with pure methylene-blue, and to remove portions of the leaves at different periods. If gentian-violet be used very pretty results may be obtained, the cells of the tentacles actively engaged in digestion being coloured red-violet, those only reflexly stimulated blue-violet; but the plants only live a short time in solutions of this stain. To obtain the differential stain mentioned, a small piece of any nitrogenous material should be placed on a leaf before immersion, and the leaf examined before all the tentacles have become inflected on it.

Fig. 8 shows the masses of aggregated protoplasm in the terminal gland of a tentacle of a plant grown in the manner described. Another point may be mentioned with regard to the colour of the stimulated

THE GLANDS OF THE MARGINAL TENTACLES OF DROSERA ROTUNDIFOLIA.

FIG. 7.

Photo, A. L. G.] (× 300.) [*Copyright.*

A terminal gland of an unfed plant grown in a weak solution of methylene blue. The nuclei of the cells surrounding the inner and denser portion are alone stained.

FIG. 8.

Photo, A. L. G.] (× 300.) [*Copyright.*

A terminal gland (*A*) and stem (*B*) of tentacles of *Drosera* grown in a weak solution of methylene blue to which some proto-albumose had been added. Note the intense staining of the cells of the gland, and of the masses of aggregated protoplasms in the stem.

cells. Even to the naked eye the glands engaged in digestion appear deeper in colour, due to the aggregation of their contents, while if an entire leaf, on which a small particle of proteid has been placed an hour or two before, be mounted, unstained, in Canada-balsam, after removal of the chlorophyll with alcohol and clearing with a volatile oil, only those glands which have been in direct apposition to the proteid retain their reddish colour. The fact that cells directly engaged in digesting and absorbing food stain red with gentian-violet seems to indicate that they are acid in reaction, and it is interesting to note that the parenchymatous cells of the pedicels exhibit this reaction as strongly as those of the glands themselves. The stronger the stimulation the further down the pedicels does this phenomenon occur.

Aggregation of the protoplasm of the cells in *Drosera*, therefore, occurs after stimulation of the glands, either directly or indirectly, is synchronous with the movement of the tentacles, does not necessarily indicate increased secretion either of an active or inactive juice, but when the terminal gland is acting accompanies the secretion of a peptic ferment and a greater supply of a vegetable acid, the cell contents apparently becoming acid in reaction. Probably the process of aggregation has some influence on that of inflection, causing a decrease in bulk in the cells to the inner side of the tentacle, re-expansion occurring through the elasticity of the outer cells whenever the contraction of the inner cells has ceased. It must, however, be stated that no change in the size of the different cells can be made out under the microscope. If the small sessile glands above described, which are scattered over the surface of the leaf, be examined after immersion in a proteid solution, the protoplasm of the two or four cells which go to form them will be found to be aggregated in a similar manner. There is little doubt but that they serve to digest and absorb the portions of the food which have sunk down to the immediate surface of the leaf, out of the reach of the glands at the ends of the tentacles.

Both the subjects of digestion and absorption in *Drosera* have been touched upon in the description given of the inflection of the tentacles and the aggregation of protoplasm in the cells. But a few points remain which deserve notice. The secretion of the glands before stimulation is neutral, after stimulation acid, but contains no ferment unless the stimulant be of an organic nature containing nitrogenous matter. A very close parallelism exists between the digestive power of the secretion of *Drosera* and that of the mammalian stomach.

T:s. *(Compiled from Darwin.)*

Class of Stimulant.	Digestion.		Notes.
	cretion.	Degree.	
1. *Physical.*	no ferment	Moderate	....
	ial, neutral	None	....
	....	....	Killed, tentacles bent back
	....	....	Paralysed, not killed
	....	....	Leaves more active after
	....	....	Often only some of the tentacles inflected
2. *Insoluble.*	no ferment	Moderate	On single tentacles
Inactive substances.	). do.	Do.	Do. do.
3. *Soluble.*	Active	Do.	Placed on leaf
a. *Nitrogenous.*	Do.	Strong	On single tentacle
1. Organic.	....	....	....
	....	....	....
	....	....	Leaves quickly killed
	Active	Slight	....
	Do.	Strong	....
	Do.	Slight	....
	Do.	Very slight	Artificial Casein is really insoluble
	Do.	Strong	....
	Do.	Slight	....
	'resent	Probably inactive	....
	Active	?	Leaves killed
	ry active	Strong	Soluble only after digestion
	Active	Do.	....
	no ferment	None	....
2. Inorganic.	....	....	With crystals leaves were killed
	....	....	Minimum amount able to excite movement 0·00000328 m.gr.
	....	....	....
b. *Non-nitrogenous*	no ferment	None	....
1. Organic.	....	....	....
2. Inorganic.	....	....	Many of those causing rapid inflection acted as poisons
	....	....	Gallic, Tannic, Tartaric, and Citric had no effect
	ent, but an-gonised	None	....

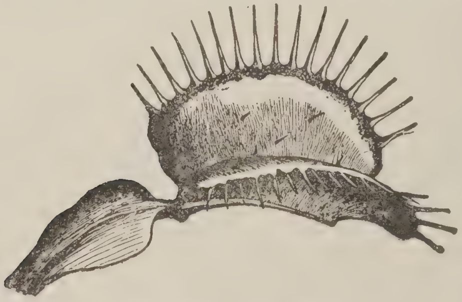
In Table VII. the results of some observations on the effect of the lower proteids and proteid derivatives are given, from which we may conclude that the glands of the *Drosera* only respond to proteids of a certain class, and only if further digestion is called for. Serum-globulin, for instance, produces only a slight degree of excitation, nuclein or nucleic acid acts as a poison, and peptone is absorbed so quickly that the leaf on which it is placed soon dies from a surfeit. The albumoses proved to be very stimulating and were entirely absorbed in course of time; no poisonous effects, similar to those described as occurring in animals after ingestion of these substances, were observed. Among the class of proteid derivatives urea acts as a poison, except in very minute doses; kreatinin and tyrosin are not absorbed. Asparagin appears to be absorbed to some extent, but the reaction of the leaves to its stimulus is not so marked as in the case of albumin or albumoses.

There are several other species of *Drosera*, differing much in size and form, but the phenomena of digestion in all of them is practically the same as in *D. rotundifolia*.

Another member of the *Droseraceæ* merits some attention, *Dionæa muscipula*, commonly called Venus's fly-trap (Fig. 9).

FIG. 9.

DIONÆA MUSCIPULA (VENUS'S FLY-TRAP).



(Meade Smith, after Darwin.)

Side view of leaf, showing marginal spines and sensitive bristles on upper surface of both lobes.

A native of North Carolina, it bears bilobed leaves on a foliaceous footstalk. The two lobes are placed at a little less than a right angle from one another and present two to four small pointed processes directed towards the opposite lobe. The upper margins of the lobes are broken up into many long, sharp, and rigid bristles, so placed that they interlock when the

TABLE VII.—*The Reaction of Drosera to Proteids and Proteid Derivatives.*

Class of Stimulant.	Stimulant.	Inflection of Leaves.				Solution.	Aggregation of Protoplasm.	Digestion.		Notes.
		Beginning.	Height.	Degree.	Close.			Secretion.	Degree.	
1. Proteid.	Raw, dry egg-albumin free from globulin	30 secs.	3 hours	Considerable	4-5 days	Slow, 12 hours	Marked	Active	Great	—
	Serum-globulin	5 hours	3 days	Incomplete	6 days	Never complete	Not well marked	Active	Slight	Very little digested
	Proto-albumose	15 secs.	45 mins. (in 24 hours leaf concave)	Complete	12 days	6 mins.	Very marked	Very active	Great	—
	Very small piece on single tentacle	13 secs.	$1\frac{3}{4}$ hours	Complete	3 days	—	Very marked	Very active	Great	—
	Deutero-albumose	15 secs.	75 minutes	Almost complete	7 days	4 mins.—absorption delayed	Very marked	Active	Moderate	Leaf often injured
	Peptone	? 7 mins.	35 minutes	Slight	Leaf killed	$1\frac{1}{2}$ mins.	Slight	Active	?	Leaf killed in 15 hours
	Nucleic acid	13 mins.	18 hours	Considerable	26 hours	None	Moderate	Slightly active	Almost nil	Leaf killed in 48 hours
	Albuminate of iron	—	Indefinite	Very slight	—	15 mins.	Marked	Active	Slight	—
2. Proteid Derivatives.	Pure urea in crystals; small crystal	20 mins.	40 minutes	Moderate—leaf concave	Leaf killed	10 mins.	Slight only	Very acid	Large amount	Leaf killed
	Do., very minute crystal on central tentacles	45 mins.	4 hours	Slight	21 hours	1 minute	Slight	Acid in 1 minute	Considerable	Leaf dry and healthy in 21 hours
	Kreatinin	Few minutes	65 minutes	Moderate	20 hours	30 mins.	Marked in tentacles touching, none in others, even if bent.	?	?	In 20 hours leaf dry, remains of kreatinin crystallised on its surface
	Tyrosin	None	None	None	None	None	Doubtful	? No increase	—	—
	Asparagin	30 secs.	6 hours	Considerable but local	3 days	13 hours	Marked	Active	Moderate	—

lobes close. As long ago as 1768 Ellis described the structure and functions of Dionæa very correctly in a letter to Linnæus, who declared it to be the most wonderful of plants (*miraculum naturæ*), but was of opinion that the flies caught by it were only enclosed accidentally. The sharp processes on the surface of the lobes are composed of elongated cells, containing a very active protoplasm, and rest on a pad of small cells. The spines themselves are rigid, but the basal pads act as hinges, allowing them to be bent down on the surface when the lobes close on one another. The upper surface of the lamina is also covered with small, short-stalked glands, very similar to those of *Pinguicula*, formed of about twenty-eight polygonal cells, and filled with a purple fluid. They secrete a digestive fluid in response to appropriate stimuli, and also have the power of absorption. Small stellate hairs are borne on the edge of the leaf between the sharp teeth, and also on the under surface. They are generally composed of eight arms, and are of a reddish-brown or orange colour. The rigid processes on the blade have neither the power of movement *per se*, nor of secretion, but are exquisitely sensitive to a momentary touch. If the point of a hair fixed in a handle be brought in contact ever so gently with one of them the lobes rapidly close. They are not, however, so easily affected by prolonged pressure as the tentacles of *Drosera*. Nor are they stimulated by placing drops of proteid or ammonium carbonate solutions on them. The lobes do not close, and no aggregation of the protoplasm of their cells occurs under these circumstances, though Darwin, by immersing cut-off filaments in solutions of ammonium salts, observed this phenomenon spreading up the filament, the reverse of what takes place in *Drosera*. Neither the heaviest shower of rain nor the strongest gale has any effect on the leaves. The impulse proceeding from the tips of the processes cannot be transmitted along vascular bundles, for they possess none, and Darwin, by severing the bundles in the lobes, showed that movement still occurred, though more slowly. As in *Drosera*, the impulse is transmitted in all directions through the cellular tissue, the rate being governed largely by the length of the cells and the direction of their longer axes. During the contraction of the lobes Burdon Sanderson discovered that the normal electrical current in the leaf and footstalk became disturbed, in the same manner as in the muscle of an animal during its contraction. A positive current nor-

mally runs from the base to the apex of the lamina, another current running in the opposite direction in the petiole. Great alteration in the intensity of these currents follows excitation of the leaf and precedes its movement. Munk has corroborated and extended the observations of Sanderson on this point.

Although the sensitive filaments respond to the slightest touch and cause a rapid closure of the lobes, soluble nitrogenous matter if applied directly to the glands brings about the same movements, but much more slowly. The lobes when closed in on digestible objects continue to exert a slight pressure on them during digestion; if the captured body is inutile this action does not occur. The movement of the lobes appears to be due to contraction of their cells, especially of those near the mid-rib. Re-expansion, whether the leaf has caught anything or not, is effected gradually, the commencement varying with the nature and size of the substance enclosed. In like manner it is apparently due to the expansion of the previously contracted cells. Re-expansion commences in a few hours after closure from mechanical irritation or the enclosure of solid non-nitrogenous bodies, and is complete in from thirty-two hours to three days. After the capture of a fly or other insect the lobes remain closed for several days, fifteen to twenty-four, many indeed never re-open, but wither and die. For several days longer these leaves do not respond to stimuli, in fact, even in a state of nature, the most vigorous plants are seldom able to digest oftener than twice or thrice during their lives. Those leaves, on the other hand, which have closed in response to a touch, or to the contact of insoluble bodies, are ready to close again even before complete expansion. The prey is caught by the rapid closure of the lobes, the glands of which secrete an active and acid juice on stimulation with a trace of dissolved nitrogenous matter. Unlike the glands of *Drosera*, they do not secrete before stimulation, nor do they act unless the stimulant be nitrogenous and soluble. The secretion is acid, due to formic acid, is strongly antiseptic, and contains a peptic ferment. Lindsay overfed several leaves with meat until they died of a surfeit, but the meat inside the leaves kept perfectly fresh whilst that outside putrefied. Unlike *Pinguicula*, all the glands secrete a digestive fluid on localised stimulation, not only those in contact with it, and this secretion may be so great

as to trickle down the footstalk. Absorption is carried on by the same glands, and, in the case of small pieces of egg-albumin, and the like, is complete. Fraustadt, indeed, was able to colour the contents of the gland-cells and their nuclei by feeding leaves with albumin dyed with aniline-red.

Dionæa is therefore chiefly remarkable for the delicacy of its motor mechanism, which is entirely specialised for the one purpose and has no power of secretion or absorption, for the rapidity with which the lobes close, and for the ease with which the leaves are killed by the very objects they are so wonderfully adapted to capture.

Aldrovanda vesiculosa.—This plant is practically a minute aquatic variant of *Dionæa*, and resembles *Utricularia* in possessing no roots and in producing hibernating buds. De Sassus, in 1861, first recorded the fact that the leaves of *Aldrovanda* are irritable, while Stein found in 1873 that they open under a high temperature (they are usually found closed in Europe), and when touched close again. Cohn and Delpino have observed numbers of crustaceans and larvæ caught between the lobes of the leaves.

The leaves are arranged in whorls round the stem, terminating in four to six rigid bristles, which probably serve to protect the delicate, translucent wings of the bilobed leaf growing in their midst. The lobes open only to about the same degree as a mussel shell. They are semicircular in shape, the inner half (also flatly semicircular) is composed of three layers of cells supporting colourless glands with footstalks and numerous finely pointed hairs similar to those of *Dionæa*. The outer portion is thinner, and bears a number of small quadrifid processes, like those of *Utricularia*, but no glands. The edges of the laminæ are turned slightly in, and are furnished with sharp indentations, turned inwards, which serve when the leaf shuts to render the escape of the prey more difficult.

The mechanism of *Aldrovanda* is the same as that of *Dionæa*. The hairs on the inner part of the leaf are sensitive, and possess both a basal and medial articulation. When they are touched the lobes close rapidly, the hairs bending at the articulations and thus avoiding injury. The glands towards the centre secrete an active digestive juice, and absorb the results of its action, while the quadrifid processes, according to Darwin, serve to absorb excrementitious products in the same manner as the processes of *Utricularia*.

CLASS III.—CARNIVOROUS PLANTS WITH TRAPS FOR THE CAPTURE OF INSECTS.

The third class of plants which possess organs adapted for the capture and digestion of insects is represented by the well-

FIG. 10.
NEPENTHES EDWARDSIANA.

(By permission of Mr. H. J. Veitch.)

The figure illustrates the position in which the pitchers grow when attached to the leaves. The lids are only slightly ajar, as is usual in young plants.

known genus *Nepenthes*, the so-called "pitcher-plants." Plants belonging to this class contain cavities or chambers into which their prey is enticed, and which are provided with a copious

fluid secretion possessing digestive powers. The order of the *Nepenthaceæ* (Figs. 10 and 11) may be taken as the type of the class. This order consists of herbs or half-shrubby plants with alternate leaves which, when perfect, have a long stalk terminating in a pitcher with an articulated lid. The pitcher may be considered to be a dilatation of a gland at the top of the mid-rib of the young leaf. The flowers are diœcious, with a 4-merous perianth. The embryos in the numerous seeds are enclosed in a fleshy perisperm. The members of the order are natives of the tropical parts of Asia, while one is found in Madagascar, and another in the Seychelles. Other members of the family inhabit Australia and New Guinea. Thirty-six species are at present known. They flourish only on marshy ground on the margins of small pools or brooks in damp primeval forests. The young plants spring from the boggy ground in rosettes which are almost identical with those of *Sarracenia*. The leaves which succeed the cotyledons, forming a similar rosette above them, rest their lower portions on the mud, while the upper parts curve upwards, carrying at their extremities a scale-like lamina resembling a cock's comb. This covers a narrow opening into a cavity in the swollen petiole. A green lobe with several coarse projecting processes may be seen on each side of the aperture. As the plant grows, leaves of an entirely different character appear clothing the long, slender stem. These leaves are long and lanceolate, the mid-rib being prolonged into a sinuous tendril, the end of which expands into the pitcher. The tendrils grasp and coil round any body which they may meet, thus hanging the pitcher, suspended at the extremity, upon a branch or other body growing at the edge of the pool. As the plant grows it may climb to the tops of trees of moderate height, clinging to the branches of the underwood and to the stems of the trees.

As stated above, the pitcher must be regarded as an excavated portion of the petiole or of the mid-rib, the lid being formed by the lamina, as in *Cephalotus* and *Sarracenia*. The lamina is only slightly changed when compared with the wonderful development of the petiole. The size of the pitchers varies with the species, from the large pitchers of the *Nepenthes rajah*, spacious enough to contain a pigeon, to the smaller examples of the *N. ampullaria*. The majority of the species possess pitchers measuring from 10 cm. to 15 cm. in height, those of the *N. rajah*, however, may reach 50 cm.,

with an orifice 10 cm. in diameter, expanding below to 16 cm. In the *N. ampullaria* they are only from 4 cm. to 6 cm. high. Before arriving at maturity the lid remains in close apposition to the rim of the pitcher, and while in this condition

FIG. 11.

A PITCHER FROM NEPENTHES DICKSONIANA.

(By permission of Mr. H. J. Veitch.)

Showing a pitcher attached to a long stalk which represents an elongated mid-rib of a leaf; the stalk grows downwards, the pitcher upwards. The variegated surface of the pitcher wall is well shown, with the lid at the apex.

is often covered with brightly coloured hairs. They may be of a rusty golden hue, or may look as if powdered with flour, as in the *N. albo-marginata*. As they become mature the hairs drop off, either entirely or in part, and the lid rises up. Both

the pitchers and the lids are invariably of a bright colour, and at a little distance almost exactly simulate flowers. Indeed, they look very like the flowers of the *Aristolochiæ*, a genus akin to them, and also to be found in tropical forests.

No better description of these plants can be given than that of Kerner in his *Natural History of Plants*, translated by Oliver:—

"The bright pitchers of *Nepenthes*, visible from afar, are sought, just as flowers are by insects, and probably by other winged creatures as well; and this occurs all the more because there is a secretion of honey by the epidermal cells upon the under surface of the lid, and on the rim round the mouth of each pitcher. The swollen and often delicately-fluted rim, in particular, drips and glitters with the sugary juice; and it would be permissible in this connection to speak of a honeyed mouth and sweet lips in the most literal sense of the words. Animals which suck honey from the lips of *Nepenthes* pitchers wander, as they do so, only too readily upon the interior surface of the orifice. But the inner face is smooth and precipitous, and rendered so slippery by a bluish coating of wax that not a few of the alighted guests slip down to the bottom of the pitcher and fall into the liquid there collected. Many of them perish in a short time; others try to save themselves by climbing up the internal face of the pitcher, but they always slip again on the polished wax-coated zone, and tumble back once more to the bottom. In large pitchers the involute rim of the aperture is in addition armed with sharp teeth, which are pointed downwards and bristle in front of such of the unlucky victims in the pitfall as try to emerge."

The walls of the pitchers may be described as being divided into three zones. The upper one is narrow and close to the rim; as we have already seen, it is studded with epidermal honey-cells, below which are ranged one or more circular rows of spinous processes pointing downwards inside the cavity. The second zone of the internal wall is covered by an exceedingly smooth epithelium which secretes a small quantity of wax. The lower third of the pitcher forms the third zone, which is about half the depth of the second. In it are found thousands of special gland cells which secrete a watery fluid with a very weak acid reaction. The quantity of this liquid may reach many cubic centimetres in some of the larger varieties. It has a slightly acid taste even if obtained from a pitcher into which no insects have fallen, though some say that its reaction is neutral under these circumstances. But as soon as the body of an animal or a piece of meat is dropped in, the fluid is secreted in larger quantities, and with a more distinct acid reaction. The secretion of the fasting pitcher has no power of igesting proteid substances, unless some acid, organic or

mineral, be added to it. The fluid obtained after an insect has fallen into the trap, on the other hand, practically acts like the gastric juice of the mammal on albuminous bodies.

Vines mixed the secretion of two pitchers of *Nepenthes sedeni* (about 12 cm.) with three drops of hydrochloric acid, and, later, with an equal volume of water. Although the secretion had been taken from fasting specimens, when thus treated it was able to gradually digest relatively large quantities of blood-fibrin, estimated at 8 c. cm. Analysis of the fluid in a pitcher which has captured an animal shows that it contains several organic acids, such as malic, citric, and formic, in addition to a ferment which, like pepsin, is only capable of digesting proteids in acid solutions. The actual acid made use of in digestion in *Nepenthes* has not been accurately determined, but that it may be formic acid is shown by the fact that the inactive fluid from an empty pitcher is capable of digesting albumin if a few drops of that acid be added.

The digested portions of the animals captured are absorbed by special cells round the bottom and lower part of the pitchers.

In addition to the acids present in the secretion, Voelcker found potassium chloride and the carbonates of sodium, magnesium, and calcium. Lawson Tait stated that he could separate from it two substances, each possessing great anti-fermentative powers, and each necessary to digestion, after the addition of an acid. One of these he termed "Droserin," and regarded it as an analogue of pepsin; the other, "Azerin," a transparent, straw-coloured solid precipitated by alcohol, comparable to ptyalin. Droserin, or similar bodies, may be regarded as the peptic ferment common to all carnivorous plants; while Azerin, a rapidly deliquescent substance, may act by rendering the secretion of the plants more wetting. For example, a fly falling into water never gets completely wetted, probably owing to the sebaceous character of the secretion of its epidermal cells, while a fly falling into a fluid containing Azerin rapidly becomes soaked through and drowned.

Cephalotus follicularis, a plant allied to the Saxifrages and known as the Australian pitcher-plant, possesses means for the capture of insects and for their subsequent digestion practically identical with that which obtains in *Nepenthes*.

Lathræa squamaria, or the Toothwort, is one of the most remarkable of the group. It is destitute of chlorophyll, lives underground, and is a true saprophyte, extracting its nourishment from the roots of flowering plants, except for the brief annual period during which it sends up a few flower-bearing shoots. The underground stems are white and fleshy, and are covered throughout their entire length with thick squat leaves placed closely together. Examination of one of these leaves reveals a structure unique in the vegetable world. Each leaf is so bent on itself that what appears to be the back is in reality the bent upper half of

the anterior face of the lamina, ending in an involute tip close to the stem, and immediately below the leaf-stalk. The true dorsal surface can only be seen on removal of the free involuted tip, and is comparatively very small. Between the tip of the leaf and the stem five to thirteen, generally ten, minute canals communicate with the air, and open into cavities in the substance of the leaf, formed by the involution just mentioned. These cavities are placed close together but do not communicate with each other. They are all longer than broad, and have irregularly sinuous walls. The walls are lined with the usual epithelial cells, but are studded with two forms of glands. The one, composed of two convex cells placed like a dome on a large, flat cell, are comparatively few in number; the other, formed by two globular cells carried on a short stalk, are very numerous. The stalked glands when stimulated protrude through pores in their thick walls delicate protoplasmic threads, which are exactly analogous to the filaments sent out by the *Rhizopoda*. The sessile dome-shaped glands, which are very similar to those present in *Drosera*, and on the under surface of the leaves of *Pinguicula*, probably act in absorbing the products of digestion. The openings into these chambers are so small that only minute animals, such as *Infusoria*, *Amœbæ*, and the like, can penetrate into the cavities. Although no evidence of any secretion from the glands of *Lathræa* has been directly established, all the proteid constituents of their prey soon disappear. The protoplasmic hairs probably serve to retain, and perhaps to kill, the animals which enter the cavities, the sessile glands to absorb the albuminoid portions. The latter, indeed, are each connected by vessels with the main fibro-vascular bundles of the leaves, the stalked glands are not.

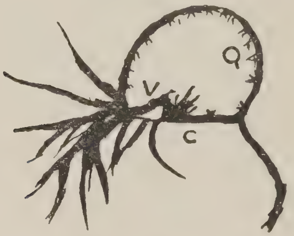
As *Lathræa* is a parasite deriving the largest part of its nutriment from the roots of deciduous Angiosperms by means of special suckers, and as it is destitute of chlorophyll, its supply of nitrogenous material is very small, and its power of converting carbon dioxide or the crude bodies derived from the sap of its host meagre. As an underground plant, growing at a depth which frost seldom reaches, and therefore active during the whole year, it has continuous opportunities for capturing animalculæ, and indeed obtains from them a large quantity of proteid material. In this way the deficit of nitrogen, due to its other habits, is equalised.

Bartsia Alpina.—One of the *Scrophulariaceæ*, *Bartsia* acts in a very similar manner to *Lathræa*. The latter, however, is a pure parasite, while *Bartsia* draws its nourishment from the ground by root-hairs, from the roots of adjacent plants by suckers, and from minute animals by cavities contrived in subterranean buds. These buds are formed in autumn, and in spring send up aerial shoots richly supplied with chlorophyll. They are formed by scales, arranged in four rows, which overlap one another like tiles. Only the upper part of the back of each leaf can be seen, the lower half being covered by the leaf below, the anterior surface closely pressed to the lower portion of two leaves of the next row. The anterior surface is strongly concave, and the edges are turned slightly back. The leaves are so arranged that the curved out margins of two leaves approximate closely together and touch the anterior surface of the leaf of the scale below, thus forming two cavities bounded by the anterior surface of the lower leaf, and the outer portions of the posterior surface of the two inner leaves. In this way each leaf covers two ducts, one on each side of the mid-rib, and forms at the point where its evolute margin begins to be overlapped by the middle of the leaf below two small openings into them. One wall of the recess or duct, namely, that formed by the posterior surfaces of the two higher leaf-scales, bears a number of glands, sessile and stalked, identical with those in the cavities of *Lathræa*. These recesses, thus cunningly contrived between the leaf-scales of a subterranean bud, serve, by the capture of infusoria, to supply the plant with a sufficient store of nitrogenous material at a time when all vegetable life at the high altitudes where it lives is at a standstill. In the habitat of *Bartsia* the activity of plant life above the ground may be limited to two months. The extra supply of nitrogen obtained from minute animal forms in the soil enables it, when its spring-time comes round, to build up an aerial stem, leaves, and flowers in a short space of time, while if this extra supply were cut off it would be unable to draw sufficient of the necessary elements for its rapid growth either from the air, the soil, or surrounding plants.

The remaining plants which may be included in Class III. do not, strictly speaking, digest their prey, but only absorb the products of decomposition or fermentation. As they obtain part of their food in this way they must be mentioned here, but as no true digestion occurs the account must be short.

The *Utriculariæ* (Bladderworts) form the largest group in this section of carnivorous plants. The members of the group are rootless plants which float in the foul and stagnant water of ponds and ditches. As winter approaches the terminal leaves enlarge and form rounded buds, while the rest of the leaves and the stem die, their air-spaces fill with water, and the whole plant sinks to the bottom. In spring, when the water becomes warmer, the buds break off from the old stems and rise to the surface. Here they soon develop two rows of lateral branches, covered with much divided filamentous leaves bearing numerous small bladders. A leaf may terminate in as many as thirty separate points, each tipped with a short,

FIG. 12.
UTRICULARIA NEGLECTA.



(From a pen-and-ink sketch by the Author.)

Section of a bladder (× 3) of the Bladderwort, *Utricularia neglecta*. *C*. Under wall thickened to form a cushion on which the free edge of a thin valve (*V*) rests. *Q*. Quadrifid absorption cells projecting into the interior of the bladder.

straight bristle, small notches on the sides of the leaves bearing similar bristles. The part that most concerns us is the bladder, and that borne by *Utricularia neglecta* may be taken as the type (Fig. 12). The bladders of this plant are translucent, of a greenish colour, about 2.54 mm. in length, and spring from the leaf-stalk, generally near its base, supported by short foot-stalks. Two or three are usually found on each leaf.

The walls of the bladders are made up of two layers of cells, the outer polygonal and large, the inner both elongated and short, the short cells bearing quadrifid processes. Between some of the larger cells of the outer surface small rounded cells may be seen supporting short conical projections surmounted

by two terminal hemispherical cells. The bladders, which are usually filled with water, have a convex dorsal surface ending in two prolongations, made up of rows of chlorophyll-containing cells, and each carrying an "antenna" formed of six or seven long multicellular bristles. The bladder, indeed, resembles a "hermit-crab" in a most curious manner. (See Fig. 12.) Between the processes bearing the two antennæ the entrance into the interior of the bladder is situated, covered by its valve. Three to seven multicellular processes project outwards from each side of the entrance, forming, with the bristles of the two antennæ, a hollow cone, the apex of which is filled by the valve. The valve itself is extremely like a cusp of the aortic valve in the human heart attached to the wall of the bladder throughout a semicircle, and presenting a free, straight margin, slightly projecting in the centre. The free margin of the valve rests on a thickened rim of the internal bladder wall, termed the collar, and can thus only open inwards. Cohn describes it as being made up of prolongations of the two layers of cells which form the bladder walls. It bears two pairs of bristles rising from near the free posterior margin, and is covered with three kinds of glands: stalked with oblong heads (round the fixed margin), short, with large, spherical, two-celled heads (at the free edge), and almost sessile, with transversely elongated heads (over the middle surface of the valve). These glands possess the power of absorption, but probably do not secrete. The ventral surface of the "collar" is covered with several rows of bifid processes, pointed towards the posterior end of the bladder.

The bladders seem to be admirably adapted for the capture of small aquatic animals, chiefly of crustaceans, such as *Cypris*, *Daphnia*, and *Cyclops*, although the reason why they should enter in is by no means clear. No fewer than twenty-four crustaceans have been found in a single bladder. It may be that the bristles surrounding the entrance suggest a safe retreat to small animals, who, accustomed to search every crevice in search of food, penetrate the opening into the bladder, or, as Darwin suggests, the transparency of the valve may attract by the spot of light which it forms. By whatever means minute animals are induced to pry into the cavity, the edge of the thin elastic valve forms a perfect trap. Mrs. Treat, of New Jersey, was fortunate enough to observe the whole process. She concluded that the valve possessed no irritability, the animals caught simply pushed the thin, elastic edge of the valve away from the inelastic collar, and gradually contrived to enter the cavity. Whenever the valve was free it closed again in virtue of its elasticity. Solid, inanimate bodies, if placed on the surface of the valve, are occasionally

enclosed, probably due to a slow bending of the surface, similar to that often observed in colloid substances. Animals, however, enter by their own movements, the head acting as a wedge. The animals captured by *Utricularia* are not digested. They die as a rule in a few days, probably owing to exhaustion of oxygen, and shortly afterwards are resolved into a muddy brown decaying mass swarming with the micro-organisms of decomposition. If the quadrifid and bifid processes which project from the small angular cells of the inner wall are examined under the microscope at a time when no decomposing animal matter is present in the bladder, their protoplasm appears to be quite transparent, save for a minute, faintly brown particle exhibiting Brownian movements. When the bladder contains animal remains the cells of these processes are filled with brown irregularly moving masses of aggregated protoplasm. Salts of ammonium in solution cause this aggregation, as also does a fresh solution of urea, but only in a moderate degree. The glands situated on the surface of the valve, and those already mentioned as interpolated between the large polygonal cells of the outer surface of the bladder, exhibit changes of a similar character when brought in contact with putrid infusions or solutions of ammonium salts, except that no true aggregation of protoplasm occurs in their cells, and that a solution of urea acts much more powerfully. Cohn asserted that these external glands secreted a slimy fluid, but the statement has not been corroborated, and they must be regarded simply as absorptive organs, those round the valve extracting nitrogen from any fluid which may escape from the bladder, those on the exterior absorbing nitrogen from the foul water around them. It is doubtful if any ferment is secreted by the processes on the interior wall; a ferment which hastens the process of decay may be. The presence of such a body is unlikely, but not inherently impossible.

One of this group, *Utricularia nelumbifolia* (Brazil), deserves a separate and passing note. *Tillsandsia*, a member of *Bromeliaceæ*, the Pine-apple order, possesses small cavities in front of each leaf which become filled with rain-water. Many varieties of small animals live in these little cisterns, swimming about in the water, while the majority of the cisterns contain a single *Utricularia nelumbifolia*. The bladders of this plant are very similar to those described above, and act in the same way. A remarkable feature is the mode by which it is propagated; for not only does the plant produce seeds, but it also sends runners in the direction of the nearest *Tillsandsia*, which dip their points into the water and give origin to another plant. Among the other members of this family are *Utricularia montana* (Brazil), a subterranean variety, and with bladders only 1 millimetre in diameter; *U. amethystina* (Guiana); *U. Griffithii* (Malay, Borneo), only .7 millimetres in diameter, and with no quadrifid or bifid processes; *U. cærulea*, *Orbiculata*, and *Multicaulis* (India). The methods for the capture of minute animals, and for the absorption of the nitrogenous derivatives

of their decay, are very similar to those in *U. neglecta*, and their modifications are not of sufficient interest to call for separate discussion.

Closely akin to *Utricularia* is the curious genus *Genlisea*. The leaves of *Genlisea ornata* are of two kinds, spatulate and utriculiferous. The latter forms pitfalls for small animals by means of a small bladder situated at its lower and blind end, a long, narrow, cylindrical, and hollow neck, and two long twisted processes which spring from each side of the narrow orifice. The twisted processes are formed by lateral prolongations from the lip of the orifice, and their structure may be understood if they are described as similar to a piece of ribbon wound spirally round a thin cylinder with its edges in contact, and then pinched up so as to form a spiral crest like the thread of a screw. The inner surface of the spiral crest is furnished with short incurved bristles projecting inwards at right angles to the line of junction. The long, hollow neck is lined throughout with transverse rows of thin transparent hairs pointed downwards, the tip of each hair being formed by a separate cell. If the neck be opened, the rows of hairs rising from small transverse ridges exactly resemble a paper of pins. Between these transverse ridges there are numbers of four- or two-celled papillæ, corresponding apparently with the bifid processes in *Utricularia*. The inner surface of the utricule is similarly supplied with hairs, which are short, close together, and confined to the upper part, and with glandular papillæ, formed of four cells, and situated for the most part in the lower segment. From this description it is evident that when a small animal has entered either the tip of one of the lateral arms, or the orifice between their bases, it can only move downwards, its return being prevented by the points of innumerable bristles. In whatever part of the trap the animal dies absorbent glands are present to ingest the products of its decay, the whole mechanism resembling a very complicated eel-trap.

Genlisea Africana and *G. aurea* (Brazil) present similar structures, but the plants of another species, *G. filiformis*, are apparently provided with bladders resembling those of *Utricularia*, growing from their rhizomes or root-stalks, but without utricules on the leaves, as in the three previous species.

Among the other plants which capture insects by means of traps, but which do not digest their prey, may be mentioned *Heliamphora nutans*,

several varieties of *Sarracenia* and *Darlingtonia*. In *Heliamphora* and *S. purpurea* the leaves are transformed into ascidia arranged in rosettes, resting their bases on the ground, and then turning up near the apex. The pitchers are of considerable size in the middle, but contract towards the orifice, where their walls pass into laminæ concave from above down. These laminæ serve to catch raindrops which flow down into the ascidia, and also to attract insects, both by reason of their bright colour and from the fact that they bear glandular hairs which secrete honey. The inner wall of the ascidium is covered, as in so many of the carnivorous plants, with projecting cells arranged like the scales on the back of a pike. These cells point downwards and present an extremely slippery surface on which any animal that ventures to explore the cavity, attracted by the honey on the laminæ, slips and is precipitated into the water. The animal is soon drowned and its body decays. The products of decomposition are absorbed by the epidermal cells at the base of the ascidium. It is uncertain whether the fluid filling the bottom of the pitcher is composed simply of rain-water, or whether it contains some secretion from the glands. It has no digestive power, but produces alterations in the captured animals in a much shorter time than pure rain-water is able to accomplish. It may be that some substance akin to "Azerin," shown to be present in *Nepenthes* and serving to engulf and macerate insects in an unusually short space of time, is secreted by the glands at the lower part of the pitcher.

Summary.—After the foregoing brief description of the principal carnivorous plants, a short note may be added on the attributes which distinguish them as a class and from one another. Table VIII. gives a summary of the properties which they have in common and the differences between them. It will be readily seen that all stages are represented, from the immobile *Drosophyllum* to the elaborate *Dionæa*. *Drosophyllum* has only a sticky secretion wherewith to capture its prey. *Dionæa* possesses three distinct and dissociated actions, sensitive filaments to record the presence of an insect, leaf-lobes to capture, and glands to digest it and to absorb the products of digestion. The larger number digest nitrogenous matter by means of an acid secretion containing a ferment, the others merely absorb the products of the decomposition of albuminous materials, with the exception of *Aldrovanda*, which appears to be able both to digest and to absorb nitrogenous matter from fresh and putrid solutions. The behaviour of the different species towards solutions of urea serves to indicate the nature of their absorptive power. The glands of *Pinguicula*, *Drosera*, *Dionæa*, and *Nepenthes* are indifferent to urea, those of *Utricularia* absorb it, while the glands of *Aldrovanda* are not stimulated, although the quadrifid processes on the outer segments of its leaves are able to absorb it.

TABLE VIII.—*Showing the Different Characteristics of the Carnivorous Plants.*

	Movements.			Trap.	Secretion.			Absorption.		Attraction.	Chief Victims.
	Presence.	Cause.	Mechanism.		Before and after Stimulation with Nitrogenous Bodies.		After Non-nitrogenous bodies.	Matter.	Agent.		
Drosophyllum	None	....	....	Viscid fluid	Acid	Acid and ferment on contact not increased in amount.	Acid, no ferment, not increased in amount.	Products of nitrogenous digestion	Secreting glands	....	Flies, seeds and pollen
Pinguicula	Present. Edges of leaves	Non-nitrogenous bodies slight, nitrogenous moderate	Impulse from secreting glands	Do.	Neutral	Acid and ferment *only on contact*	Neutral	Do.	Do.	....	Do.
Drosera	Present. Tentacles	Touch, inorganic and organic bodies rapid or marked	Impulse from glands	Do.	Neutral	Acid and ferment *both with contact and reflexly*	Acid and ferment	Do.	Do.	Colour, odour ?	Do.
Dionæa	Present	Touch, rapid, organic bodies slow	Sensitive non-secreting hairs. Secreting glands	Rapid closure of leaf-lobes	None	Acid and ferment *both in glands in contact and in others*	None	Do.	Do.	Colour	Flies
Nepenthes	None	....	....	Pitcher with secreted fluid, no valve, spines projecting down.	Slightly acid	More acid, ferment present	Slightly acid	Do.	Do.	Colour, honey	Flies
Lathræa	None	....	....	Tortuous cavities in leaves, no valve	None	Present, acid and ferment	None	Do.	Do.	?	Minute insects
Bartsia	None	....	....	Spaces between immature leaves.	None	Present, acid and ferment	None	Do.	Do.	?	Infusoria
Aldrovanda	Present	Touch, rapid, organic bodies ?	Sensitive non-secreting hairs. Secreting glands	Rapid closure of leaf-lobes	None	Acid and ferment both in glands in contact and in others	None	Products of (1) digestion and (2) decomposition of nitrogenous bodies.	(1) Secreting glands (2) quadrifid processes	?	Flies
Utricularia	None	....	....	Bladder with valve, filled with water	None	None	None	Products of decomposition only	Quadrifid and bifid proc'sses, sessile glands on outside.	Spot of light on valve	Crustacea
					(N.B —Last three may secrete a body lowering surface tension.)						
Genlisea	None	....	....	Spiral processes, bladder with spines projecting down	None	None	None	Do.	By glands in pitcher and papillæ of processes	?	Minute animals
Sarracenia	None	....	....	Ascidium with rain-water, no valve, spines	None	None	None	Do.	By glands at bottom of ascidium	Colour, honey	Flies and creeping insects

It cannot be too strongly insisted that the mode of absorption of nitrogenous compounds by the various members of the carnivorous plants is merely a habit induced by the poorness of the soil in which they live. In many other plants the supply of nitrogen is probably increased by the absorption of traces of ammonia and nitric acid from rain-water. The water, again, which collects in the hollows of the leaves in saxifrages and *Bromeliaceæ*, or at the junction of opposite leaves in many *Compositæ* and *Dipsaceæ*, is always brown coloured, due to the decaying bodies of insects which have fallen into it. Often this water is absorbed with some of the nitrogenous matter, the plants only differing from *Sarracenia* in this respect in that they possess no regular trap or decoy. As has been already stated, the conversion of insoluble and indiffusible bodies into soluble and diffusible compounds is a universal attribute of all living organisms, and is an indispensable preliminary to assimilation. All plants are able to convert or digest proteids and carbo-hydrates; the carnivorous class are only remarkable for their property of performing digestion outside instead of inside their cells. That the capture of insects and the assimilation of the products of their digestion aids the plants of carnivorous habits has been clearly proved by F. Darwin. Many contrary opinions have been held, based largely on measurements of growth and the fatal results which follow overfeeding. The important point which F. Darwin discovered is that the increase occurs mainly in the reproductive organs of the plants, not so distinctly in the leaves and stalk. The seeds of some plants of *Drosera* which were fed regularly surpassed those of unfed plants, kept under identical conditions, by 240 to 100 in number, and 157 to 100 in weight. The benefit derived by carnivorous plants from the utilisation of the products of the digestion of nitrogenous bodies is indisputable.

CHAPTER IV.

Digestion in Animals.

Development of the Alimentary Canal.—Of the Associated Glands.
Anatomy of the Alimentary Canal.—Mouth—Teeth—Tongue—Salivary Glands—Stomach—Intestines.

THE DEVELOPMENT OF THE ALIMENTARY CANAL.

We now leave the vegetable kingdom to turn to our main subject—digestion in animals.

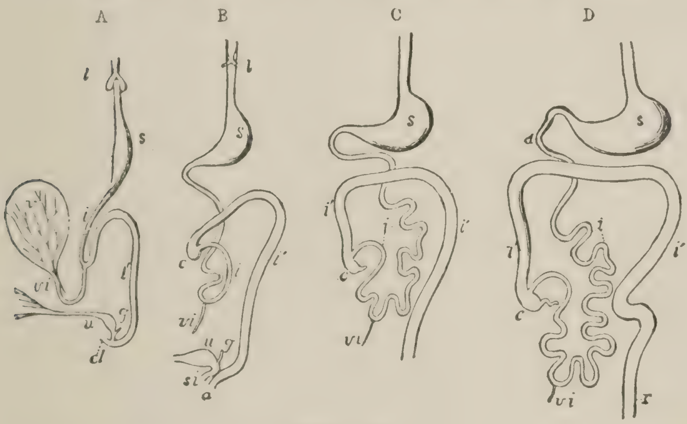
The different parts of the alimentary canal, and the various organs associated with it, are developed, in the first instance, from the hypoblast or inner layer of the embryo, although elements from the visceral layer of the mesoblast or middle layer are included in almost all of the organs as well. Twelve hours after the commencement of incubation of an egg the first trace of the formation of the chick appears as the "primitive streak." In the rabbit seven days elapse before the impregnated ovum shows a similar line. A transverse section through the ovum at this stage reveals the presence of three layers of embryonic cells, the epiblast or outer, the mesoblast or middle, and the hypoblast or inner layer. The alimentary canal at first is formed by a simple inflection of the inner layer, its walls consisting only of epithelial cells derived from that layer of the blastoderm. It soon exhibits traces of a division into three parts. The anterior part, or *foregut*, is that enclosed by the anterior or cephalic fold, and corresponds to the pharynx, gullet, stomach, and duodenum of the adult. The *hindgut* is the part included in the caudal prolongation of the embryo, and the *midgut*, which in time develops into the small and large intestine, is still in the form of a wide and

open groove. The foregut and hindgut are of tubular form, and are closed at the anterior and posterior extremities of the embryo by the epiblast and mesoblast, which are inflected inwards at the points which afterwards become the mouth and the anus. The foregut, as development proceeds, becomes dilated in one portion of its length to form the future stomach; the upper and lower parts remain tubular. Up to this time it has occupied a position in the long axis of the body. The dilated portion, however, soon turns over to its right side, though still in the long axis, then gradually becoming more dilated, it assumes the oblique position of the adult. The tubular portion below this shows signs of the development of the liver, pancreas, and spleen. The midgut is, as mentioned above, at first in the form of an open groove communicating with the yolk-sac. It is soon transformed into a tubular organ, still communicating by a duct with the umbilical vesicle. When it first assumes a tubular form, the midgut is straight, but increasing in length, it takes the shape of a loop bent forwards to the navel. The loop is connected with the tissues of the body walls by a prolongation of the mesoblast, termed the mesentery. The hypoblast, according to Remak, furnishes the glandular and epithelial elements of the intestine, the mesoblast, the muscular and connective tissue, and the blood-vessels. Schenk has attributed the glandular elements to the mesoblast also. At the apex of the loop a protrusion of the bowel wall signifies the differentiation of the cæcum from the small intestine. As the small intestine extends it is thrown into coils. The large gut is at first the smaller of the two. The hindgut only represents the anus and its adjacent parts in the mature animal. The outer coats of the pharynx and œsophagus are furnished by the mesoblastic layer of the embryo, but below them the mesoblast divides into two portions—the inner or visceral mesoblast forming the outer wall of the alimentary canal and its peritoneal covering; the outer, or parietal mesoblast, the parietal peritoneal tissue. The mouth is not formed from the primitive hypoblastic layer. The involution of the outer epiblast over a point corresponding with the anterior extremity of the alimentary tube in course of time comes in contact with the tubular pharynx, a solution of continuity occurring at the posterior arch of the fauces. The lining membrane of the mouth and nose is therefore derived from the

epiblastic layer of the embryo. The anus is similarly formed from a posterior epiblastic involution. The liver first appears as a small mass of cells on the lower surface of the duodenum. The mass soon becomes hollow and lined with epithelium from the intestinal hypoblast. This cavity represents the future common bile duct. The cells of the original mass are mesoblastic, but solid cylinders of hypoblastic cells soon penetrate between them. These cell processes unite with each other terminally

FIG. 13.

THE DEVELOPMENT OF THE ALIMENTARY CANAL.



(From Quain.)

A, Alimentary canal, in an embryo of five weeks.
B, Do. do. at eight weeks.
C, Do. do. at ten weeks.
D, Do. do. at twelve weeks.
l, Primitive lungs connected with pharynx; *s*, Stomach; *d*, Duodenum; *i*, Small intestine; *i'*, Large intestine; *c*, Cæcum and vermiform appendage; *r*, Rectum; *cl* in *A*, the Cloaca; *a* in *B*, anus distinct from *si*, the sinus uro-genitalis; *v*, the yolk sac; *vi*, the vitello intestinal duct; *u*, bladder urachus; *g*, the genital ducts.

and laterally, communicating with each other and enclosing mesoblastic tissue in which blood-vessels connected with the umbilical vein develop. Hollow processes sprout out from the solid cylinders through the liver substance and represent the larger hepatic ducts, the solid processes becoming the lobular tissue of the liver. In the fœtus the umbilical vein communicates with the vena cava by one branch, a second and larger branch joining the portal vein. After birth the umbilical vein

becomes obliterated up to its connection with the portal vein; the branch to the vena cava also disappearing. The pancreas, like the liver, is first represented by a mass of mesoblastic cells attached to the wall of the duodenum close to but to the left of the hepatic rudiment. It may be detected on the fourth day in the chick. A diverticulum of hypoblastic cells from the bowel wall penetrates the mesoblastic mass, forming the rudiments of the pancreatic duct and of its branches. Some observers credit hypoblastic columns of cells pushing in among the mesoblast with the formation of the glandular cells, the mesoblast affording only the vessels and connective tissue. This view is the most probable, but, as in the liver, the question as to how far the hypoblast enters into the composition of the gland, or how much of it is derived from mesoblastic elements, is still a matter of controversy.

The anal invagination of the epiblast mentioned above is comparatively slightly marked in mammals. In rabbits the connection between the hind-gut and this invagination becomes patent about the twelfth day, in birds not until the fifteenth. In all species the uro-genital and anal apertures are at first conjoined in one opening. After the fifth week in all the mammals, with the exception of the *Monotremata*, the anal orifice becomes distinct from the urinary and genital opening.

SURVEY OF THE ANATOMICAL FEATURES OF THE ALIMENTARY CANAL.

The anatomical details of the alimentary canal in the various members of *Animalia* differ with the nature and digestibility of the food. The teeth vary with the actions, gnawing, tearing, and grinding, required to thoroughly masticate the substances taken in; the form of the lips with the mode of prehension of the food; and the length and complexity of the alimentary canal with the nature, the digestibility, and the nutritive value of the substances consumed.

The method by which the food is seized exerts a marked modifying influence upon the form of the mouth and the structure of the associated organs. Thus, among *Monotremata* who live on small insects and molluscs, the *Ornithorhynchus*, or duck-mole, captures the aquatic organisms on which it lives by means of a beak, very similar to the bill of a duck; while the only other member of this order, the *Echidna*, or porcupine ant-eater, possesses a long and flexible tongue covered with a sticky secretion, by which it captures the insects forming its food.

The kangaroo uses its forelegs to bring the food to its mouth. The *Sirenia*, comprising the manatee and dugong, live on sea-weeds which they obtain by cropping with their fleshy lips. In the *Cetacea*, the minute marine organisms forming the food of some of the species are strained off from the sea water by means of enormous meshworks of whale-bone or baleen. In the horse the upper lip, in the ox the tongue, and in the sheep and goat both the upper lip and the tongue, are used to bring the food under the action of the teeth. The lower lip in the pig serves to gather the food rendered accessible by the spade-like action of the snout. Carnivorous animals, as the dog, cat, seal, etc., seize their prey with their teeth, while in many the tongue is furnished with horny papillæ which serve to remove the flesh from the bones of the animals caught. The rodents use their teeth in obtaining food, their teeth being adapted for cutting and gnawing. One of the most peculiar and specialised organs for the prehension of food is the proboscis or trunk of the elephant, which must be regarded as a result of evolution based upon the advantage derived by an animal able to reach the foliage on which it feeds, at a height inaccessible to most other species. In the apes and in man the arms and hands serve to lay hold of the food and bring it to the mouth.

The Mouth.—The lining membrane of the mouth is, as we have seen, formed by the epiblastic or outer layer of the embryonic cells. The lips are covered with a very sensitive, dry mucous membrane, continuous with the skin. The mucous membrane is supplied with numerous vascular papillæ, containing nerve filaments and nerve end-bulbs. Inside the mouth the lips and cheeks are covered by a moist, smooth mucous membrane attached in the middle line anteriorly to the mucous membrane of the gums by two folds or *fræna*, the upper of which is the larger. Numbers of small mucous glands open on the inner surface of the lips and cheeks, termed *labial* and *buccal* glands respectively. They appear only to secrete mucus. Corresponding with its epiblastic origin, the mucous membrane lining the mouth is formed of scaly epithelium on the surface, and of prickle cells, like those of the skin, in the deeper layers. The gums are formed of dense connective tissue firmly attached to the periosteum covering the jaws.

In the *Monotremata* and in some of the *Edentata* the teeth are wanting, as in the whale-bone whales; they have no need of them.

The Teeth.—Among the mammalian orders provided with teeth three classes may be described :—

1. Carnivorous animals with teeth adapted for tearing and gnawing flesh.
2. Herbivorous animals—
   - A. The *Rodentia*, with incisor teeth adapted for cutting and molars for grinding.
   - B. The *Ruminantia*, which are provided with cutting incisors in the lower jaw only, and with grinding molars.
   - C. In the *Solipedes* and *Pachydermata* cutting incisors are present and grinding molars, while in many the lower canines are absent. In the elephant one pair of upper incisors is enormously developed.
3. Omnivora.—The dentition of omnivorous animals forms a link between that of the carnivora and herbivora.

The *Mammalia* generally are supplied with two sets of teeth, a milk or temporary, and a permanent set. A tooth is developed from the epiblastic or outer layer of the embryo which lines the mouth, by a projection downwards of its epithelium. It is not, as might be imagined, a product of the bone in which it is afterwards embedded. (See Figs. 14 and 15.) At first the downward growth of the epithelium is in the form of a line or groove along the border of the jaw, when it is called the *common enamel-germ*. The epithelial cells contained in it develop more rapidly at the points corresponding to the future milk-teeth; these growths, becoming separate in time, are known as the *special enamel-germs*. A papilla rises from below, projects into each special tooth-gum, which forms a cap or covering over it. The epithelial elements become the dental enamel, while the papillæ represent the dentine and pulp of the teeth. About the sixteenth week in man a secondary bud develops from the neck of each follicle, composed of epithelial cells, to become later the ten anterior permanent teeth. About the fourth month of fœtal life thin caps of dentine are formed on the pulps of the milk-teeth, covering the outer edges of the papillæ, and shortly after enamel begins to be deposited over them. The dentine is formed of large cells, with long filamentous processes situated in the outer parts of the pulp. It is at first uncalcified, but

later nodules of lime salts are deposited in its matrix, forming at length a uniform hard tissue. The epithelial cells of the enamel-germ covering the dentine now become calcified *in situ*,

FIG. 14.

SECTION ACROSS THE UPPER JAW OF A FŒTAL SHEEP.

(Quain, after Waldeyer. × 50.)

1, Enamel germ dipping down into the mucous membrane, where it is half surrounded by a semi-lunar shaped mass of denser-looking tissue, the germ of the dentine and dental sac; 2, palatin process of the maxilla.

FIG. 15.

SECTION ACROSS THE UPPER JAW OF A FŒTAL SHEEP.

(Quain, after Kölliker.)

A special enamel germ, *f*, becoming flask-shaped; *c*, *c*′, epithelium of mouth; *f*, neck of enamel germ; *f*′, body of flask-shaped enamel germ.

the outer cells growing meantime and calcifying progressively from within outwards. The eruption of the temporary teeth is preceded by absorption of part of the bony wall surrounding it. As the tooth emerges bony tissue is again deposited

round its neck and fangs, forming a socket. The permanent teeth which succeed the milk-teeth are developed from the epithelial buds already mentioned, in the same way as their predecessors, but growing below and behind them. As the permanent teeth increase in size, the cement and dentine of the milk-teeth are attacked by large cells called osteoclasts and become absorbed. Thus their absorption does not proceed from pressure by the rising teeth alone. The six posterior permanent teeth develop in a similar manner to the milk-teeth.

A tooth is thus composed of a vascular pulp, containing blood-vessels and nerves, of dentine secreted by cells in the pulp, and of enamel formed of calcified epithelial cells. The enamel is made up of very hard microscopical columns of phosphate of calcium with a trace of calcium fluoride, 4.4 per cent. of calcium carbonate, 1.3 per cent. of phosphate of magnesium and other salts, only 2 to 3.5 per cent. of animal matter, and 0.2 per cent. of water. The individual enamel columns measure about $\frac{1}{5000}$th of an inch, .005007 millimetre. On the surface of the enamel in unworn teeth a thin horny membrane is found, "the skin of the teeth," serving as a protective covering. The dentine, on the other hand, consists of much less dense tissue. Its percentage composition is as follows:—Water, 10; phosphate of calcium, 66.7; carbonate of calcium, 3.3; phosphate of magnesium, etc., 1.8; organic matter, 18.2. (Bibea.)

Dentine is penetrated by numbers of fine, parallel tubules, about $\frac{1}{4500}$ inch in diameter, and twice or thrice that distance apart from each other. Lomas has observed the tubules running into the enamel in the teeth of marsupials, and also, but less distinctly, in man.[1]

Owing to the fact that the arrangement of the articulation between the upper and lower jaw differs in the various mammalian orders, the possible movements of the teeth of the lower jaw against those of the upper are dissimilar. In the *Carnivora*, for example, the lower jaw is narrower than the upper, and the upper canines overlap the molars, so that only an up-and down motion is possible. No grinding movements can be performed. The meaning of this is not far to seek, as the carnivora feed on easily digested matters, which they tear into pieces of a convenient size and bolt with little or no preliminary mastication. All their teeth are suited for cutting or tearing the food. The incisors are large and sharp, the canines long and pointed, while the molars are irregularly ridged or tuberculated, and, as they overlap like the blades of shears, act as cutting not grind-

[1] The description of the development and anatomy of the teeth has been partly taken from Quain's *Anatomy*.

ing agents. The *Rodentia* are characterised by the back and forward movements of their jaws, and the great size of their incisor teeth. These teeth have a layer of hard enamel anteriorly and a somewhat softer portion of dentine behind. The unequal rate at which these two portions wear away causes the teeth to retain a sharp chisel-shaped free surface. The teeth of the *Rodentia* are peculiar in that they continue to grow during the whole life of the animals, as do the molars of the ox, while in all other mammals the second teeth reach their full development in a short time after eruption, cease to grow, and even undergo little or no natural repair. The molar teeth in the *Rodentia* are marked with transverse ridges across the flat crown. There are no canines. The forward and backward movements of the jaws serve to press the sharp cutting edges of the incisors against those in the opposite jaw and so to cut through the grass used as food, while the same movements cause the transverse ridges of the lower molars to grind and bruise it against those in the upper jaw. There are no incisors in the upper jaw of the *Ruminantia*, the incisors of the lower jaw being opposed by a firm fibro-elastic pad. The incisors have sharp cutting edges, and the molars present flat crowns transversely ridged. The canines are generally absent, or are confined to the lower jaw. The chief point worthy of note as regards the movements of the jaws in the *Ruminantia* is the extensive power of lateral motion. Strictly speaking, it is circular in nature, the axis of the lower jaw crossing that of the upper, and is alternative—that is to say, the lower jaw is moved to the right, then back to the centre, and to the right again for a certain period of time, for half-an-hour or longer, when the deviation changes to the left. A backward and forward motion is also used. In the other members of the *Herbivora*, the *Solipedes* and *Pachydermata*, a great contrast between the dentition present exists. In the *Solipedes* a similar but less extensive lateral motion of the lower jaw occurs, incisor teeth are present in both jaws, canines (in the stallion, but absent in the mare) and irregularly ridged molars are also present. Only the upper incisors are found in the *Pachydermata*, taking the form of long tusks which project from each side of the jaw. The molars are very large and few in number, with flat crowns transversely ridged and tuberculated. As the elephant procures its food by means of its trunk no teeth are required for the purpose of seizing or cutting, and all the necessary mastication can be performed by

molar teeth adapted for grinding. The *Omnivora* possess teeth adapted both for cutting and grinding, and can move the lower jaw in the three directions mentioned above.

The dentition of man may be looked upon as being midway between that of the *Carnivora* and the *Herbivora*. If anything, it inclines more to the carnivorous type than the herbivorous, owing to the constant presence of canine teeth and the character of the molar crowns, which are tuberculated and not ridged. For convenience, the numbers of the various kinds of teeth present in the different classes are generally represented by formulæ, the "dental formulæ." In such a formula the number of each variety of teeth present on one side only of each jaw is often given, and the number multiplied by two gives the total number present. In the formulæ, *i.* indicates incisor, *c.* canine, *pm.* pre-molar, and *m.* molar teeth.

The following table gives a few of the most important of the formulæ among the *Mammalia*.

TABLE IX.—*Dental Formulæ in the Mammalia.*

CARNIVOROUS.

Dog.

$$\text{i. } \frac{3\text{-}3}{3\text{-}3} \text{ c. } \frac{1\text{-}1}{1\text{-}1} \text{ p.m. } \frac{4\text{-}4}{4\text{-}4} \text{ m. } \frac{2\text{-}2}{3\text{-}3} = 42$$

Cat.

$$\text{i. } \frac{3\text{-}3}{3\text{-}3} \text{ c. } \frac{1\text{-}1}{1\text{-}1} \text{ p.m. } \frac{3\text{-}3}{2\text{-}2} \text{ m. } \frac{1\text{-}1}{1\text{-}1} = 30$$

Seal.

$$\text{i. } \frac{3\text{-}3}{2\text{-}2} \text{ c. } \frac{1\text{-}1}{1\text{-}1} \text{ p.m. \& m. } \frac{5\text{-}5}{5\text{-}5} = 34$$

Hedgehog.

$$\text{i. } \frac{3\text{-}3}{3\text{-}3} \text{ c. } \frac{0\text{-}0}{0\text{-}0} \text{ p.m. } \frac{4\text{-}4}{2\text{-}2} \text{ m. } \frac{3\text{-}3}{3\text{-}3} = 36$$

HERBIVOROUS.

Ox.

$$\text{i. } \frac{0\text{-}0}{3\ 3} \text{ c. } \frac{0\text{-}0}{1\text{-}1} \text{ p.m. \& m. } \frac{6\text{-}6}{6\text{-}6} = 32$$

Horse.

$$\text{i. } \frac{3\text{-}3}{3\text{-}3} \text{ c. } \frac{1\text{-}1}{1\text{-}1} \text{ p.m. } \frac{3\text{-}3}{3\text{-}3} \text{ m. } \frac{3\text{-}3}{3\text{-}3} = 40$$

Rabbit.

$$\text{i. } \frac{2\text{-}2}{1\text{-}1} \text{ c. } \frac{0\text{-}0}{0\text{-}0} \text{ p.m. } \frac{3\text{-}3}{2\text{-}2} \text{ m. } \frac{3\text{-}3}{3\text{-}3} = 28$$

Rhinoceros.

$$\text{i. } \frac{1\text{-}1}{1\text{-}1} \text{ or } \frac{0\text{-}0}{0\text{-}0} \text{ c. } \frac{0\text{-}0}{0\text{-}0} \text{ p.m. } \frac{4\text{-}4}{4\text{-}4} \text{ m. } \frac{3\text{-}3}{3\text{-}3} = 32$$

OMNIVOROUS.

Man.

$$\text{i. } \frac{2\text{-}2}{2\text{-}2} \text{ c. } \frac{1\text{-}1}{1\text{-}1} \text{ bicusp. } \frac{2\text{-}2}{2\text{-}2} \text{ m. } \frac{3\text{-}3}{3\text{-}3} = 32$$

Hog.

$$\text{i. } \frac{3\text{-}3}{3\text{-}3} \text{ c. } \frac{1\text{-}1}{1\text{-}1} \text{ p.m. } \frac{3\text{-}3}{3\text{-}3} \text{ m. } \frac{3\text{-}3}{3\text{-}3} = 40$$

The dentition of the members of the *Carnivora* given above yields an approximate mean of

$$\text{i. } \frac{3\text{-}3}{3\text{-}3} \text{ c. } \frac{1\text{-}1}{1\text{-}1} \text{ p.m. } \frac{4\text{-}4}{3\text{-}3} \text{ m. } \frac{3\text{-}3}{3\text{-}3}$$

The hedgehog being insectivorous, has no need of canines.

The *Herbivorous* animals yield an average formula approaching to:

$$\text{i. } \frac{2\text{-}2}{2\text{-}2} \left(\frac{0\text{-}0}{3\text{-}3} \text{ in Ruminantia} \right) \text{ c. } \frac{0\text{-}0}{0\text{-}0} \text{ or } \frac{1\text{-}1}{1\text{-}1} \text{ p.m. \& m. } \frac{6\text{-}6}{6\text{-}6}$$

The typical *Omnivorous* formula contains:

$$\text{i. } \frac{2\text{-}2}{2\text{-}2} \text{ or } \frac{3\text{-}3}{3\text{-}3} \text{ c. } \frac{1\text{-}1}{1\text{-}1} \text{ p.m. } \frac{2\text{-}2}{2\text{-}2} \text{ m. } \frac{3\text{-}3}{3\text{-}3}$$

The Tongue.—The tongue is almost entirely composed of muscular tissue covered by mucous membrane. On the under surface this covering is similar to and continuous with that of the inner aspect of the cheeks and lips. The mucous membrane of the upper surface is modified to subserve the function of taste. It is covered with papillæ of three kinds, which in turn possess numerous secondary papillæ under the epithelial cells.

The smallest and most numerous papillæ, termed *conical*, are most numerous anteriorly, gradually diminishing in numbers towards the base. They are, as their name implies, small conical eminences, and are arranged in lines diverging from the central line or raphe.

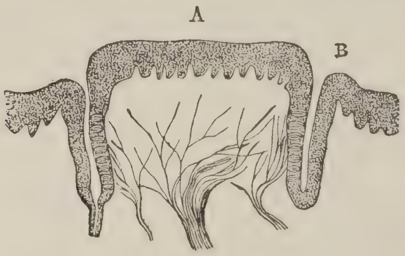
The conical papillæ possess a denser epithelial covering than the other forms, and are of use in the mechanical action of the tongue upon the food. In many of the carnivorous animals these papillæ become enormously developed, enabling their possessors to scrape the flesh off the bones of their prey.

The second group of papillæ, the *fungiform*, are rounded in form, of a deep red colour, and are most numerous at the apex and borders of the tongue, though also scattered over the anterior two-thirds of the dorsum. Each papilla is abundantly supplied with nerve filaments.

The *circumvallate papillæ* (cf. Fig. 16) form the last group, and are much larger in size, only from seven to twelve in number, and situated in two converging rows at the base of the tongue. Each papilla is placed in a circular depression of the mucous membrane, the smaller end set in the centre of the depression and the broad flat top reaching a little above the level of the surrounding surface of the tongue. In the walls of a papilla a zone of taste-buds opens into the surrounding trench, and in some species another zone is found on the opposite wall.

FIG. 16.

VERTICAL SECTION OF CIRCUMVALLATE PAPILLA OF THE TONGUE OF THE CALF.



(Quain, after Engelmann. × 25.)

A. Papilla. *B*. The surface of the mucous membrane of the tongue, dipping down on each side to form the vallum or trench which surrounds the papilla. In the wall of the papilla, forming one side of the trench, taste-buds may be seen. The nerves of the papilla are shown running upwards and towards the taste-buds. At the bottom of the trench on the left the duct of a gland is seen to open.

These *taste-buds* (Fig. 17) open on to the surface by pores between the epithelium cells. Further in they form globular flask-shaped bodies, their outer covering composed of long flattened cells, their centre of spindle-shaped cells. The central spindle cells are enlarged about the middle to accommodate their nuclei, while their extremities are prolonged into fine processes, one of which projects through the orifice, the other communicating with a plexus of nerve filaments placed in the tissue below the taste-bud.

Flask-shaped bodies of a very similar structure are found scattered over the mucous membrane of the mouth, and even in the skin, of fishes, and are believed to serve the same

function. In the *Amphibia* the taste-buds are replaced by patches of gustatory cells interspersed among the epithelium of the dorsum of the tongue. In the rabbit and hare numbers of taste-buds are distributed in the laminæ of a structure called the *papilla foliata* situated at the base of the organ.

The mucous membrane of the tongue also contains many small glands principally grouped near the base, and some opening into the trenches round the circumvallate papillæ. These *lingual glands* secrete a watery fluid probably containing some mucus, but their function is not clear.

The body of the tongue is made up of muscular tissue

FIG. 17.

TASTE-BUDS.

(Quain, after Engelmann. × 450.)

Two taste-buds from the papilla foliata of the rabbit.

arranged in such a way that free movement of the organ in every direction is attainable.

The roof of the mouth is covered by a dense mucous membrane, which is usually corrugated to a greater or less extent. In some animals these corrugations are very prominent and serve to aid the action of the tongue in the disintegration of food, when the morsels of food are pressed against and dragged over them.

A continuation of the mucous membrane of the hard palate forms the pendulous structure, or *soft palate*, which provides a partial separation between the cavities of the mouth and pharynx.

On each side, immediately posterior to the soft palate on each side, are found the tonsils. They are composed of lymphoid tissue in which are enclosed twelve to fifteen crypts. These crypts open by a similar number of apertures on the inner aspect of the gland, and contain in their walls great numbers of lymphoid follicles identical with those described as present over the posterior part of the tongue.

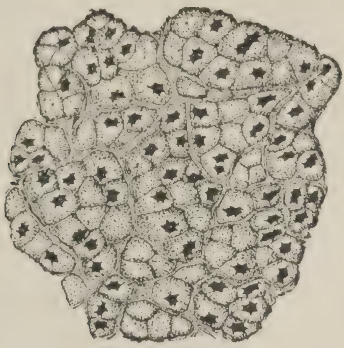
The Salivary Glands.—The salivary glands are of three distinct varieties. The first variety secretes a thin, clear, serous fluid, resembling dilute blood-serum; the secretion of the glands belonging to the second type is a viscid, mucous fluid; while the third type yields a mixed fluid composed of both serous and mucous secretion.

In the *Mammalia* the parotid gland is almost invariably a purely serous gland, and in the rabbit the submaxillary gland belongs to the same type. In man the submaxillary gland secretes a mixed saliva, but in the cat and the dog it only yields a pure mucous fluid. The sublingual gland is generally a mixed gland, but with the mucous element predominating.

The structure of the different salivary glands varies with the characters of the secretion. The serous glands of which the parotid may be taken as the type, are made up of branching alveoli or system of ducts, each main duct progressively subdividing until the terminal ducts are reached. The alveoli are united by connective tissue into lobules. On their basement membrane are placed glandular cells, with nuclei at the end next the membrane, but usually in the inactive state so filled with protoplasmic granules that the nuclei cannot be seen (cf. Figs. 18 and 19). After activity the granules disappear from all parts of the cells except close to the lumen of the tubes. In the submaxillary gland of the dog the alveoli are similarly arranged, but the cells lining the tubules when inactive are large, clear, and bulge into the tubules so as almost to occlude them. The cells are filled with mucigen, or the forerunner of mucin. After discharge the cells appear shrivelled and granular. If they are subjected to prolonged stimulation some cells may be discharged bodily with the mucus. A part of the cell may remain along with the nucleus and serve to regenerate it, or, as Heidenhain held, the cell is replaced by the growth of an adjacent marginal cell. It is possible that during secretion cells are constantly being cast off and new cells developing to take their place.

FIG. 18.

SECTION OF THE PAROTID GLAND OF THE RABBIT IN AN INACTIVE STATE.

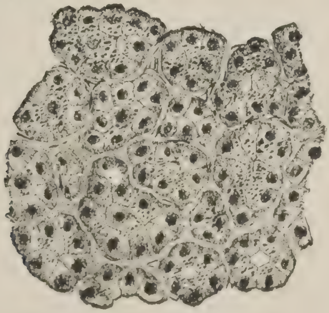


(Meade Smith, after Heidenhain.)

The cells are granular, the nucleus often indistinct owing to the number of granules, especially towards the outer part of each cell.

FIG. 19.

SECTION OF THE PAROTID GLAND OF THE RABBIT AFTER STIMULATION OF THE CERVICAL SYMPATHETIC NERVE.



(Meade Smith, after Heidenhain.)

The cells are darker; the outer parts less so than before, the inner parts more so.

In the mixed glands in man, such as the submaxillary and lingual, both serous and mucous alveoli are found, although it is not uncommon to find mucous cells and serous cells mingled in the same alveolus.

The secretion of the parotid gland is carried into the mouth by Stenson's duct, which opens opposite the second molar tooth of the upper jaw in man, and opposite one or other of the molars in animals. The submaxillary gland occupies a position to the inner side of the lower jaw and on the digastric muscle, and sends its secretion by Wharton's duct to an opening beneath the anterior portion of the tongue. The sublingual gland lies beneath the tongue reaching back from the frænum, and pours its secretion into the mouth by from eight to twenty ducts, the ducts of Rivini, immediately above the position of the gland.

In man the parotid is the largest, the sublingual the smallest of the glands. In all animals save the dog the parotid gland is the largest. In *Herbivora*, especially the *Ruminantia*, it is highly developed. As a rule the posterior salivary gland, belonging to the serous type, corresponds in size with the amount of mastication required. The anterior glands, whose secretion serves to lubricate the food swallowed before thorough mastication, are most highly developed in the carnivora and aquatic animals. But the rule is not invariable, for the ox possesses enormous submaxillary glands and relatively small parotids, while in the dromedary the former are small and rudimentary. The volume of the salivary glands in the *Herbivora* exceeds that in other species, but bears no relative proportion to the amount of saliva secreted.

TABLE X.—*The Average Weight of the Salivary Glands with the Mean Quantity of Saliva Secreted.*

Animal.	Weight of Glands.	Saliva Secreted per hour. During Mastication.
Horse	509 grammes	5000-6000 c.cm.
Ox	624 do.	6000 do.
		In the twenty-four hours.
Horse	509 do.	42 kilogrammes.
Ox	624 do.	56 do.
Dog	25 do.	86 grammes.
Man	34 do.	1.5 kilogramme.

In the hog the total weight of the salivary glands averages 305 grammes; in the sheep, 83; in the cat, 10. The parotid glands of the horse are four times as large as the submaxillary glands, but they secrete twenty-four times the amount of saliva; and the submaxillary gland of the ox, though rather larger than the parotid, or equal to it in volume, only secretes one-fourth of the quantity produced by the latter.

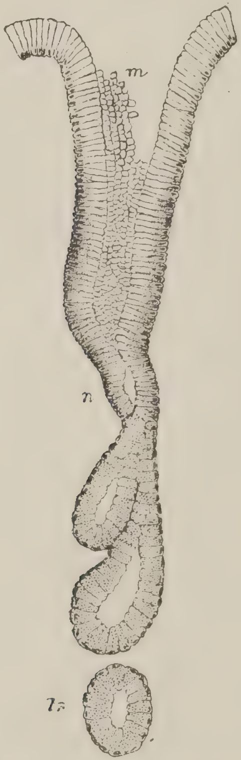
The Œsophagus.—The structure of the œsophagus is comparatively simple. It is a tube of varying length formed of three coats. The external coat consists of two layers of muscular fibres, an outer of longitudinal and an inner of circular fibres. The muscular layers are much thicker than in other parts of the intestinal canal except near the anal region. The middle coat is composed of areolar tissue and serves to connect the outer with the inner coat. The inner layer, or mucous membrane, is covered with scaly, stratified epithelium, and contains a number of racemose, branching œsophageal glands, more particularly at the lower end of the tube. They are of the character of mucous glands. Some of the variations in the form of the gullet are mentioned elsewhere (pp. 255-286).

The Stomach.—In the embryo, as we have seen, the rudimentary stomach is placed parallel to the long axis of the body. In the *Reptilia* and oviparous vertebrates this position persists, though in birds the first indication of a transverse position appears to be more fully developed. In the *Mammalia* the stomach is a simple or compound sac whose walls consist of four coats—viz., an outer peritoneal covering and three layers corresponding to those of the œsophagus. The muscular coat is formed of longitudinal, circular, and oblique fibres arranged in layers from without inwards. At the lower end of the organ the circular layer forms a thicker annular bundle or pyloric sphincter. The mucous membrane of the stomach is a soft, smooth, pink layer thrown into numerous wrinkles or folds when the stomach is contracted or empty, but with an even surface when the organ is distended. The surface of the mucous membrane is covered with columnar epithelial cells, the type of cell changing abruptly at the point of junction between the œsophagus and stomach. These columnar cells are mucigenous. While inactive they are filled with a clear mucigen—forerunner of mucus—which is discharging during digestion. When the mucous surface of the stomach is examined with the aid of a lens numerous small round openings can be seen amidst the epithelial cells. These are the mouths of the ducts belonging to the gastric glands. The glands are either simple, consisting of one tubule, or compound, and made up of two, three, or even six tubules uniting together at a common aperture. Two types of glands are described. The first type (cf. Fig. 20) is represented by the simpler *pyloric* glands, most

numerous near the pylorus, and formed by a duct lined with epithelium like that of the mucous membrane of the

FIG. 20.

A GLAND FROM THE PYLORIC REGION OF THE STOMACH OF THE DOG.



(Quain, after Ebstein. Highly magnified.)

m, Mouth of gland opening into stomach cavity, wider than in cardiac glands, narrowing at *n* to a neck, and expanding below into the active part or fundus; a cross section of this deep portion is shown below, *tr*.

stomach leading down to several terminal tubules lined by a single layer of short, finely granular columnar cells. The

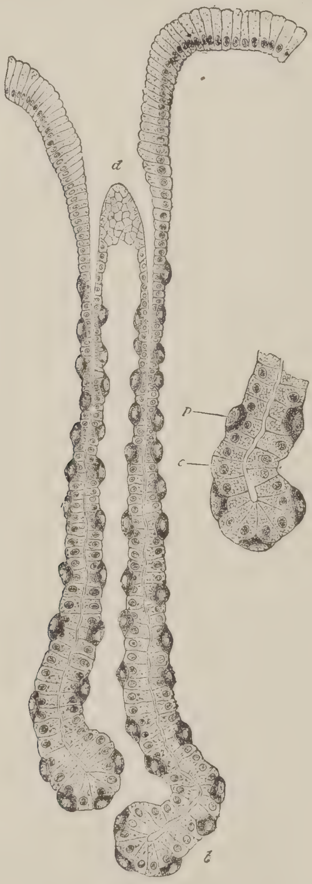
second kind of gland—the *cardiac*[1] *gland* (the fundus-gland of Heidenhain, the oxyntic gland of Langley)—is shorter and composed of one or two tubules lined by coarsely granular epithelium (cf. Figs. 21, 22). These epithelial cells were termed by Heidenhain the *principal cells*, they are also called the *central cells*. Between them and the basement membrane of the tubules *superadded*, *parietal*, or *oxyntic* cells are found. These cells are of large size, oval in form, markedly granular, and most numerous at the necks of the glands, though ceasing abruptly when the ordinary epithelium of the stomach begins. They stain deeply with osmic acid and aniline blue, and are readily recognised owing to the bulging of the basement membrane over them.

In some animals, as, for instance, the porpoise and pig, the parietal cells are contained in a special pouch of the basement membrane communicating with the main tubule by a narrow orifice. The principal cells in the bird occupy the main tubules, the parietal cells lining accessory branches, while in the *Amphibia* the cardiac glands contain no principal cells, parietal cells alone being present, but the lower end of the œsophagus is furnished with cells analogous in form and function to them. During digestive activity the central or principal cells of the cardiac glands and the cells of the pyloric tubules, which when at rest are granular throughout, present changes similar to those described as occurring in the cells of the salivary glands of the serous type; the granules partly disappear and partly congregate in the part of the cell next the lumen of the tubule (cf. Figs. 23, 24, 25). The parietal cells enlarge during the earlier periods of activity and then shrink again, but no definite change in the character of their contents has been noted. The principal cells of the cardiac glands and those of the pyloric glands are supposed to secrete pepsin, while the parietal or oxyntic cells are allotted the function of the secretion of the hydrochloric acid. The principal cells of the frog's œsophagus yield only pepsin, while the pyloric region of the stomach has been isolated, and found to afford an alkaline fluid containing pepsin. In neither region are parietal cells to be found. The cardiac glands of the frog's stomach have been found to yield a small quantity of pepsin, although

[1] The upper part of the stomach where the gullet joins it is known as the cardiac end, the body as the fundus, and the lower as the pyloric end.

FIG. 21.

A GLAND FROM THE CARDIAC END OF THE STOMACH.



(Quain, after Klein and Noble Smith. Highly magnified.)

b, Base or fundus of a tubule ; *d*, mouth of gland or duct ; on the right the bars of a tubule still more highly magnified ; *c*, central cell ; *p*, parietal cell.

wholly composed of parietal cells, so that it does not follow absolutely that one class of cell can only produce the ferment, or the acid; but it may be affirmed that the one class is chiefly engaged in the formation of pepsin, the other in the separation of hydrochloric acid from the chlorides of the blood.

FIG. 22.

GLANDS OF THE FUNDUS OF THE STOMACH IN MAN.

(Meade Smith, after Heidenhain.)

A and *A'*, when fasting; *B*, first stage of digestion—the chief cells are darker, enlarged, and becoming turbid; *C* and *D*, second stage—the chief cells have become smaller again, but are more turbid.
At *b l* in *B*, and at *a* in *C*, portions of the glands have been omitted to save space.

The Small Intestine.—The small intestine is a tortuous tube arbitrarily divided into three parts—(1) the duodenum, (2) jejunum, and (3) ileum,—from above downwards, whose walls are composed of four layers of a similar nature to

FIG. 23.

THE SUPERFICIAL EPITHELIUM OF THE GASTRIC MUCOUS MEMBRANE IN *SALMO SALAR*.

(From a drawing by Dr. Lovell Gulland. × 1000.)

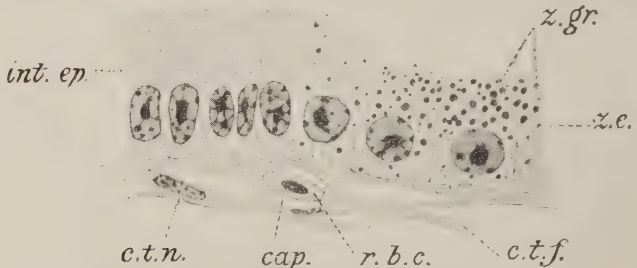
The cells show no zymogen granules.

The nuclei, with the intra-nuclear network, are well seen, and the different appearance presented by the outer zones of the cells from that of the inner zones is very distinct.

(The superficial epithelium does not form part of the actual gastric glands, but covers the non-glandular surface of the stomach.)

FIG. 24.

THE EPITHELIUM LINING THE INTERMEDIATE AND LOWER PARTS OF THE GASTRIC GLANDS OF *SALMO SALAR*.



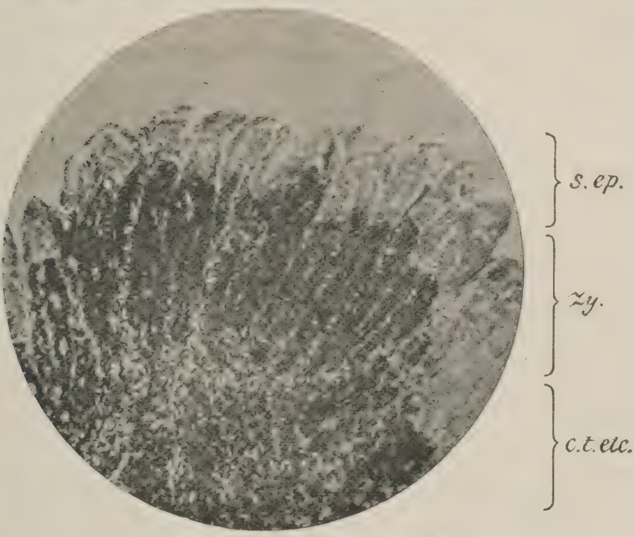
(From a drawing by Dr. Lovell Gulland. × 1000.)

int. ep. Epithelial cells of intermediate part, showing no zymogen granules; *z. gr.*, zymogen granules in lower or zymin-secreting part, *z.e.* (only some of the granules are shown for clearness); *cap.*, capillary; *r.b.c.*, red blood corpuscle.

those of the stomach. The outer, or peritoneal, covering entirely surrounds the jejunum and ileum, but only forms a partial coating over the duodenum. It is continuous along the course of the small intestine with the mesentery, which serves to convey vessels and nerves and to support the bowel. The muscular coat is divisible into longitudinal and circular

FIG. 25.

MICRO-PHOTOGRAPH OF THE GASTRIC MUCOUS MEMBRANE OF THE *SALMO SALAR*, SHOWING AGGREGATIONS OF PEPSINOGEN GRANULES.



(Photograph by Dr. Lovell Gulland.)

s.ep. Surface epithelium.
zy. Zymogen granules in the cells of the glands.
c.t., etc. Connective tissue, blood-vessels, etc.

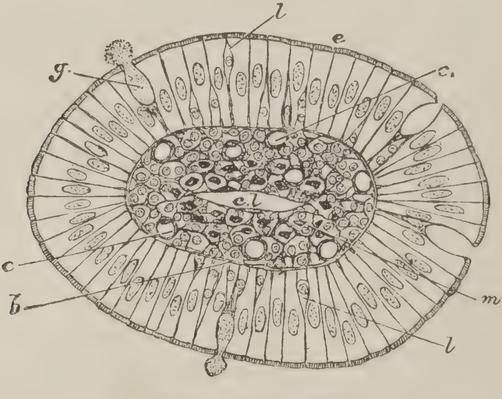
The photograph was taken from the mucous membrane of a kelt when the glands were growing again on descent from the spawning bed to the sea.

layers, and is attached to the mucous membrane by a loose areolar tissue. The surface of the mucous membrane is exactly like velvet pile in appearance, owing to the number of processes, or *villi*, which cover it. It also presents numerous wrinkles, some of which disappear on distension, while others are permanent. The permanent folds, the *valvulæ conniventes* of

Kerkring, are transverse projections of the mucous membrane, reaching in each case from one-half to two-thirds of the circumference of the bowel. The *villi* cover the whole surface and are about $\frac{1}{50}$ to $\frac{1}{36}$ inch long, and occur in great numbers in the upper portions of the small bowel, about 10 to 18 per square millimetre, compared with from 8 to 14 in the ileum. This computation yields a total number of about four millions (Krause). (Fig. 26.)

FIG. 26.

CROSS SECTION OF A VILLUS OF THE SMALL INTESTINE OF THE CAT.



(Quain. Highly magnified.)

b, Basement membrane; *c*, blood-capillaries; *e*, columnar epithelium; *g*, goblet cell with mucus partly exuded; *l*, lymph corpuscles between epithelium cells; *m*, section of plain muscular fibres; *c*, *l*, central lacteal.

Each villus consists of a prolongation of the mucous membrane of the bowel, containing blood-vessels, one or more lacteals, and a few unstriped muscular fibres. The small arteriole which enters each villus runs up the centre, breaking into numerous capillary branches when it reaches beyond the middle point of the villus. The capillaries ramify just below the basement membrane supporting the epithelial cells, and in man unite in a single vein at the tip of the villus. The vein then courses down the centre of the villus to join the venous system of the connective tissue beneath. The lacteal vessel

also lies in the centre of the villus. It is usually single in the smaller villi of man, never divided into more than two branches. In the sheep numerous branching lacteals are found. The lacteals communicate with branched cells in the areolar tissue of the villi, and with its cell-spaces. These spaces are in touch with the flattened cells of the basement membrane, from which prolongations extend between the epithelium-cells. The deeper ends of the lacteals join lymph vessels which unite in turn with the central chyle duct. The epithelium covering the mucous membrane of the small intestine is columnar in form and polygonal on cross section. The free end next the lumen of the gut is more highly refracting than the rest of the cell, and shows fine striations. The striæ are supposed to indicate either the presence of fine pores or the existence of solid rods. The remainder of the cell has a granular appearance under the microscope from the presence of numerous vacuoles in the protoplasm. Among the columnar epithelium-cells goblet or chalice cells occur which possess a mucus-forming function. The number of these mucus cells varies greatly in different animals. After a meal containing fat the columnar cells become opaque and turbid from the presence of small oil-droplets within them. Shortly afterwards the branched cells in the areolar tissue also become turbid, and finally the central lacteal vessel presents the same appearance.

Brunner's Glands.—For one or two inches below the pylorus the walls of the duodenum are studded with small glands similar in structure to the pyloric glands of the stomach, but more complex and extending more deeply into the intestinal wall. Smaller numbers of these glands are found in the lower part of the duodenum. During digestion the epithelium-cells of Brunner's glands are large and clear, becoming granular again when quiescent. In the sheep the glands form a continuous layer round the duodenal wall and appear to secrete a fluid capable of digesting proteids and converting starch into sugars. *Lieberkühn's glands* are the most numerous of the secretory structures in the mucous membrane of the small intestine. They form minute tubes, opening on the surface between the villi. Their length varies from $\frac{1}{300}$th to $\frac{1}{120}$th inch, and their diameter reaches only to $\frac{1}{600}$th inch. The tubes are lined by columnar epithelium resting on a basement membrane, among which are occasional goblet cells. They secrete the *succus entericus*, and are the main source of this

fluid. Other glands present in the walls of the smaller bowel are simply masses of lymphoid tissue; when isolated they are termed solitary glands, when grouped together in oblong patches they receive the name of Peyer's patches. Peyer's patches are more frequent in the ileum than in the bowel above it, and are placed longitudinally on the bowel-wall opposite to the insertion of the mesentery, the thin tissue membrane which serves to support the gut and attach it to the walls of the abdominal cavity.

Situated in the intestinal wall, there are two fine plexuses of nerve filaments principally connected with the superior mesenteric nerves. The outer plexus—Auerbach's—lies between the longitudinal and circular muscular fibres of the wall communicating with the inner and finer plexus, found in the submucous coat—the plexus of Meissner.

The Large Intestine.—The large intestine has the same four coats already noted as surrounding the small bowel. Of these only the mucous membrane requires separate mention. It is smooth and possesses no villi, but contains large numbers of the glands of Lieberkühn, which are larger and longer than in the small intestine. The cells lining them are largely made up of goblet or mucus-cells. In the rabbit all the cells are of this kind, in the dog every alternate one is a goblet-cell, and in man they are fairly numerous. Columnar epithelium of the ordinary type is found between them. Lymphoid nodules are scattered over the surface, similar in appearance to the solitary glands of the small intestine. The vermiform appendix, which juts out from the cæcum immediately beyond the ileo-cæcal valve, where the small and large bowel join, is a long, slender tube, the walls of which are mainly composed of lymphoid tissue. The appendix is only found in the higher mammalia and the wombat. It is not as yet known what its exact function is, but from its lymphoid structure it has been termed the intestinal tonsil. The large intestine is divided into three portions: the cæcum, the colon, and the rectum. The mucous membrane of the cæcum and colon is sacculated in many of the vertebrata, but in animals provided with a complex stomach capable of causing very complete digestion of the food, as in the ox, both these segments are smooth.

The Liver.—The liver in vertebrate animals is a large gland placed so as to intercept the blood coming from the intestinal organs before it reaches the right side of the heart. The blood

is conveyed from these organs by the portal vein, which enters the liver and subdivides into branches ending in a terminal capillary network in each hepatic lobule. These capillaries proceed from the circumference to the centre of each lobule, where they unite to form venous branches of the hepatic veins, which receive as well the blood from the hepatic artery after its circulation through the liver substance. The blood in the hepatic artery serves to nourish the liver tissue. The substance of the liver is made up of a great number of small lobules, $\frac{1}{24}$—$\frac{1}{12}$ inch (1-2 mm.) in diameter in man. Each lobule consists of hepatic cells occupying the spaces between the capillary network from the portal vein, and separated from one another by fine spaces, the commencing biliary ducts. Small canaliculi in the substance of the hepatic cells communicate with these adjacent passages. The finer vessels unite to form biliary ducts, and these in turn form the hepatic duct. Attached to the liver there is a membranous sac, the gall-bladder, from which a duct, the cystic duct, proceeds to join with the hepatic duct already mentioned, forming the common bile-duct. The common bile-duct opens into the duodenum. As the liver cells possess no cell-membrane, and are situated close or in apposition to the walls of the portal capillaries, they are in a position to receive and make use of the products of digestion contained in the blood serum with great facility. In a fasting animal the cells are granular and faintly yellow in colour, with one or two nuclei. After a full meal they are more opaque and contain masses of glycogen. The gall-bladder is lined with columnar epithelium and secretes a large quantity of viscid mucus which mingles with the bile from the liver. In the *Invertebrata*, the so-called bile is poured directly into the intestine. Among the *Vertebrata*, the *Carnivora* and *Omnivora*, and most of the *Herbivora*, *Aves* and *Reptilia*, possess gall-bladders. It is, however, absent in the *Solipedes* (horse, mule, and ass); in the stag and camel; in the elephant, rhinoceros, and tapir; in the wild boar, and some of the *Cetacea;* and among birds, in the pigeon, cuckoo, parroquet, and ostrich.

The opening of the common duct may be separate from or united with that of the pancreatic duct, but is always placed obliquely, so that pressure from the intestinal contents closes it and prevents regurgitation into it.

The Pancreas.—The pancreas is one of the most constant of

all glands in animals. It exists in most insects and fish, in all reptiles, birds, and mammals.

In the *Mammalia*, and the majority of the *Aves* and *Reptilia*, the pancreas is situated in a bend formed by the duodenum. In rodents and in the cat the duodenal mesentery is wide and the pancreas arborescent or scattered; in the dog and other mammals where the mesentery is short or absent the gland forms a thick elongated body. The pancreas communicates with the duodenum by one or two, sometimes several, ducts. The dog and rabbit possess two ducts, the upper one opening along with the bile duct into the bowel. In the cat and seal the ducts are more numerous.

The pancreas is an acino-tubular gland closely resembling the salivary glands in structure, though softer and less compact. The ultimate branches of the ducts communicate with the glandular alveoli and are lined with flattened epithelium. As these unite to form the larger ducts the epithelium becomes first cubical then columnar in character. While the gland is inactive and at the earlier stages of activity the alveoli are almost entirely filled by the secreting cells; at a later stage the shrinking of the cells causes an enlargement of the lumen. The characteristics of the secretory cells are described elsewhere (p. 122).

CHAPTER V.

Ferments and Ferment Action.

Unorganised Ferments :— Action — Theories — Berzelius — Liebig — Fischer—Bunge—Tammann—Pohl—Common Characters—Zymogens —Ptyalinogen—Trypsinogen — Pepsinogen—Rennet-zymogen—Other possible Zymogens—Glucoside-splitting Ferments—Myrosin—Emulsin. Organised Ferments: — Properties — Products — Unformed Ferments produced by Formed Ferments.

Those bodies which have received the name of Ferments may be divided into two distinct classes—the unorganised and the organised ferments. The latter class comprises all those minute types usually described as micro-organisms, each individual representing a complete and living entity capable of producing its kind. The fermentation which is caused by them is merely the result of their growth and development. Their power of digesting or simplifying complex bodies is treated of further on. The unorganised or unformed ferments are the products of living cells, and do not of themselves constitute living entities.

THE UNORGANISED FERMENTS.

Living protoplasm, whether it be in the form of a wandering *Amœba*, the active part of a vegetable cell, or the living force in an animal protoplast or cell unit, always possesses certain fermentative properties. It has the power of producing from its own constituents highly complex proteid bodies endowed with the faculty, indispensable for the continued life of the protoplast, of initiating and facilitating chemical changes in other bodies of high potential energy, whereby they are transformed into derivatives of less potential energy, without a commensurate expenditure of force. These unformed or unorganised fer-

ments—enzymes, as Kühne has christened them—are incapable in themselves of any further reproduction or increase, in direct contrast to the organised ferments, which increase and multiply in the actual course of their specific action. The organised ferments are killed by the action of alcohol, formalin, chloroform, and many antiseptics which do not prevent, though they may retard, the processes rendered possible by the unorganised bodies.

The action of an unorganised ferment or enzyme may be compared to that of oil in the working of machinery. In fact the words ferment and enzyme (from ζύμη, a ferment) are ill-suited to describe the active agents of digestion. A satisfactory term has yet to be found. Lubricant, to the author's mind, describes their action more precisely, especially as the derived substantive denotes instability as well as the property of facilitating the motion of bodies in contact. An enzyme has no power in itself to cause chemical changes in the organic compounds on which it acts. It merely renders them more unstable, allowing the primary agents—as, for instance, acids in peptic, and alkalies in tryptic digestion—to act in a state of greater dilution or at a lower temperature than they require when unaided. For instance, if albumin be boiled for a long period in a dilute solution of a mineral acid, in course of time the same changes occur in it as are much more rapidly produced at a lower temperature if a proteolytic ferment has been added. The acid is capable by itself of decomposing the albumin, but only if added in strong solution, or, if dilute, when a high temperature is maintained for a long period. When even a minute amount of pepsin is added the complex albumin molecule appears to become less stable, and a dilute solution of the acid is able to split up the molecule into smaller and more hydrated bodies.

To return to the simile of the lubricating oil: just as, in the movement of machinery, the quantity of oil used to allow of easy motion is extremely small when compared with the results obtained, so in the chemical movements termed fermentative, occurring in both plant and animal organisms, the quantity of ferment destroyed is infinitesimal and out of all proportion to the amount of work which it has enabled the chief factor in the process to achieve. Still another parallel exists; for in time the oil becomes thickened with the results of the friction of the machinery, and the wheels become clogged; while the

ferments cease to act if the products of their action are not removed by absorption or dialysis.

The underlying principle of all unorganised ferment action in nature consists in catabolic changes, whereby complex organic bodies are split up into simpler compounds, with which additional atoms of the elements of water are united.

The chief unorganised ferments which act in the processes of digestion may be divided into four classes. The action of the first class is comparatively simple, the class comprising the diastatic ferments, which act on carbo-hydrates, and the proteolytic ferments, which simplify proteid bodies. The chemical changes effected by the members of this class are elementary but extensive. The ferments of the second class, on the other hand, produce complicated chemical changes, and are exemplified by emulsin of the almond, and myrosin of mustard. This class has the power of splitting up glucosides into glucose and various other bodies. The fat-splitting ferments form the next class. By their means neutral fats are resolved into glycerine and free fatty acids. Ferments of this class occur both in plants and animals. The last class of which mention need be made is one which is represented by rennet, or the milk-curdling ferment; this also is found in both animals and vegetables. The precise mode in which rennet acts is as yet unknown, the coagulation of casein produced by it appears to be simply a molecular change, the previously soluble casein becoming insoluble in water. The coagulum formed from milk on the addition of acids differs from that produced by the milk-curdling ferment in two particulars—it is much less easily soluble in dilute acids, and contains no phosphate of lime, the coagulated casein due to the action of the ferment dissolving readily in acid media, and always containing phosphate of lime; in fact, rennet is entirely inactive if earthy phosphates are absent. In speaking of the peptonising ferments, the changes brought about by their action are described as simple, regarding them from a chemical point of view. It should be stated, however, that in plants much more profound decomposition of proteid bodies occurs when they are converted into asparagin $(C_2H_3NH_2)(COOH_2)$, and tyrosin $(C_6H_4\left(\begin{matrix}OH\\C_2H_3\end{matrix}\right.(NH_2)(COOH)$, both of which are crystalline and diffusible, requiring only some carbo-hydrate bodies and a compound of sulphur to again form

proteid molecules, an anabolic process which is performed by the living protoplasm of the cells. In animals these bodies, together with leucine and glutamic acid, are formed during tryptic digestion from proteids, but here they are by-products and forerunners of urea, rather than diffusible and soluble means of conveying nitrogenous compounds to the cells. Two additional ferments have been described as existing in the small intestine, namely, the "inverting" and the "maltose-converting" ferments. The first assists in the transformation of cane-sugar into dextrose and lævulose, the second helps to convert maltose into grape-sugar. Although it is by no means proved, it is most probable that all these actions are only rendered possible by the presence of the different ferments, the various acids and alkalies present being the active agents. All the changes induced by ferment action can be artificially produced by the aid of strong acids and alkalies, of heat, or of both combined. The action of organised ferments cannot be thus imitated. Many of the organised ferments produce unformed enzymes, some of which, as in the *Micrococcus ureæ*, have been shown to act within the body of the cell producing them. As a general rule, unformed ferments act extra-cellularly.

Theories of Ferment Action.—Berzelius was the first to ascribe to soluble ferments a "catalytic" action. Reasoning from the various reactions which platinum black—platinum in a state of extremely fine division—is capable of causing, while undergoing no change itself, he argued that mere contact in certain cases was sufficient to bring about chemical action in other bodies, with rearrangement of their elements, and without any change in the provocative substance. Subsequent research has, however, shown that the catalysing body does not remain absolutely inert. Indeed, a catalytic force which can exert kinetic, and at the same time retain all its potential energy, is opposed to every natural principle. Still this theory has its supporters, probably owing to its simplicity.

Liebig modified the catalytic theory by suggesting that ferments were complex bodies in a state of instability. They were prone to decomposition, and the changes resulting in the rearrangement of atoms started similar changes in bodies exposed and susceptible to their action. According to Liebig, the action of ferments is purely fortuitous. Others have likened

the action of ferments to the force employed in exploding a charge of gunpowder, a change from unstable to stable chemical bodies. A small amount of energy expended may produce effects quite out of proportion. But there is this objection to be taken to such a view, that the action produced by a ferment is strictly proportionate to, though immensely greater than, the quantity of ferment present, while there is no limit to the amount of gunpowder or other explosive which can be decomposed by the same initiatory force. Lately, Fischer finds the ground for ferment action in "stereochemical relations," that is in the geometrical configuration of the substances acted on. Nasse argues that if ferments are the cause of the transposition of free ions, the "leitungsfähigkeit"—conductivity—of watery solutions will be increased over that of water itself, or of watery solutions containing the ferment after it has been rendered inactive.

TABLE XI.—*Electric Conductivity.* (*Nasse.*)

The resistance of watery solutions of a ferment, after being boiled, equals	2106
Ditto, before boiling	2556
When the resistance was tested in solutions containing ferments after boiling, and bodies on which they could act, the figure was	2124
Ditto, with unboiled ferment	2082

"The increase of conductivity shown above, as occurring in the solution containing the raw ferment and fermentable substances, is to be regarded as due to an increased dissociation of water, and therefore the formation of ions by ferment action must be held as proved." Bunge, in his admirable *Lehrbuch der physiologischen und pathologischen Chemie*, concludes his description of the various changes produced by unformed ferments and the analogous changes which can be brought about by metals and living cells, thus: "We see from all these examples that our knowledge of the ferments is limited to calling them catalysing bodies. They are substances whose presence is necessary for the initiation of those chemical changes which give the impulse for an alteration of an atom-complex from an unstable to a stable substance of the same bulk. We speak of a catalytic action if the substance whose action is described as being of this nature is a known inorganic compound or a single element. If the substance, on the other hand, be of

unknown organic composition, we speak of ferment-action." That is to say, Bunge recognises that we know little about the changes brought about by inorganic catalytic processes of chemistry, and that the sum of our knowledge concerning them is the sum of all that we can confidently assert in connection with the analogous actions of organic ferments. Tammann (*Zeitschrift für phys. Chem.*, xvi. s. 271) suggests that the action of hot water and acids in producing changes in complex chemical bodies similar to those brought about by ferments may be due to transference and movements of oxygen ions. The ferments, on the other hand, are not electrolyte, but may contain certain atom-complexes in their molecules which have an affinity for certain atom-complexes in the molecules which are split up. Jacobson has lately contradicted the statement, made by Schönbein, among others, that the specific action of unformed ferments is very nearly akin to the power possessed by inert bodies, as, for instance, platinum black, of decomposing peroxide of hydrogen into oxygen and water.

Injection of the unformed ferments into the body is followed by the production of toxic symptoms, with fever and a tendency to hæmorrhages or local blood clotting. Many have suggested that these symptoms are due to the introduction of organisms along with the ferments, owing to the difficulty of sterilising them without destroying their specific action. Kionka (*Deutsch. Med. Wochen.*, 1896, No. 38) has lately shown that a solution of invertin, rendered sterile with corrosive sublimate by Geppert's method, remained active but still caused similar toxic symptoms, though to a less degree.

E. Buchner was able to produce the alcoholic fermentation of sugar by means of the fluid material expressed from large masses of yeast, and absolutely free from all living yeast cells. Neither chloroform nor a 1 per cent. solution of arseniate of sodium arrested the action. H. Buchner draws an analogy from this between alexins, unformed ferments, and toxins which may form part of the active contents of cells though not products of their metabolic processes.

Pohl (*Arch. f. Exper. Path. u. Pharmak.*, xxxviii., 1 u. 2, p. 65, 1896) draws attention to the lack of uniformity existing between the different unformed ferments, both of animals and of plants. Thus the ferment contained in liver extract can oxidise formaldehyde into formic acid,

$$\begin{matrix}H\\H\end{matrix}{>}C=O \qquad\qquad \begin{matrix}H\\HO\end{matrix}{>}C=O,$$

but is unable to form "Indo-phenolblau" from α-naphthol or phenylendiamin; while a ferment obtained from the leaves of plants, or from pine-needles, can only act conversely. So amygdalin produces indigo almost at once from the above-mentioned substances, but has no action on formaldehyde. The indigo-reaction as a test for ferment action is liable to error, and only those ferments which can oxidise aldehydes into members of the

carboxyl group answer to a test which is usually thought to be conclusive, *i.e.*, their destruction by heat.

In a work of a philosophic cast Arthus (*Nature des Enzymes*, Paris, 1896) argues that the essential nature and mode of action of enzymes, or unformed ferments, are dependent on properties of material substances rather than materialistic in themselves. He regards unformed ferment action as due to certain modes of motion in matter. The fact, however, that formed ferments can secrete enzymes capable of acting furth of their bodies, and that these enzymes gradually disappear as the fermentative action, induced by their presence, proceeds, renders the possibility of this view being in accordance with the actual mode of the action very doubtful.

The Common Characters of Unformed Ferments.—No one has succeeded as yet in obtaining any of the unformed ferments in an absolutely pure state. Owing to the difficulty of separating the ferments from the accompanying proteid bodies dissolved in an extract of the glandular tissue, or in its secretion, the opinion come to by many observers, that the ferments themselves are similar to proteids in composition, cannot be accepted implicitly. As Hammarsten remarks, it has not yet been determined whether the bodies isolated are pure enzymes, or enzymes in conjunction with albuminous bodies.

Meade Smith, in his treatise on the *Physiology of the Domestic Animals*, hazards the statement that purified ferments do not give the proteid reactions, but his statement must be received with caution, as no proof is advanced of the manner in which the specimens alluded to were purified. Schomnow and Simanowsky have lately published some analyses of pepsin obtained from the gastric juice of a dog in whom œsophagotomy had been performed, and, as well, a gastric fistula made. No saliva could enter the stomach, and the juice was obtained as secreted. The pepsin was obtained by drying the juice in vacuo, saturating with sulphate of ammonium, or by cooling to 0° Cent. The purest pepsin was obtained by the cooling process. It always gave the reactions for proteids, was easily soluble in water, and acid in reaction—giving the tests for free hydrochloric acid; it digested albumin, especially if hydrochloric acid up to 0.6 per cent. was added, and it was soluble in glycerine. When dry it was of a slight greenish-white colour, and when incinerated it yielded an unweighable quantity of ash.

Ultimate analysis gave the following result :—

TABLE XII.

	Pepsin from Cooling.	Pepsin from Sulphate of Ammonium.
Carburetted hydrogens	50.73 per cent.	50.37 per cent.
Hydrogen	7.23 ,,	6.88 ,,
Chlorine	1.17-1.01 ,,	0.89 ,,
Sulphur	0.98 ,,	1.35-1.34 ,,
Nitrogen	—	14.55-15.0 ,,

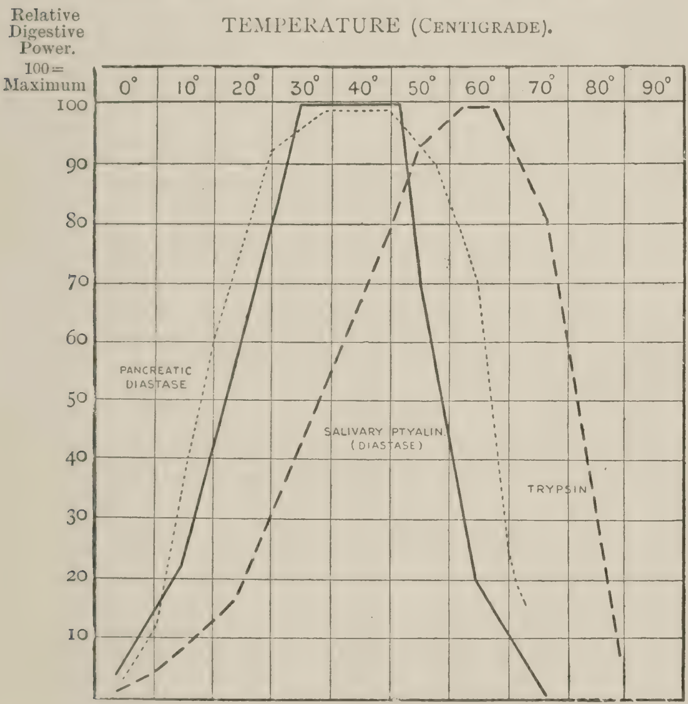
These authors conclude that pepsin is a proteid body which has a certain proportion of chlorine in its molecular structure. On the other hand, Hammarsten states that the purest specimens of the milk-curdling ferment which have as yet been obtained do not give the ordinary reactions characteristic of proteids.

We may conclude that the true chemical nature of the unorganised ferments is still unknown, but that the majority of them do not obscure by their presence, or even vary, the common proteid reactions exhibited by the extracts containing them, and that, as they are a product of the activity of protoplasm, they are either very similar in composition to proteid bodies, or are derivatives split off from them.

All enzymes are soluble in water, and probably in glycerine. Langley states, however, in a note printed in Gamgee's *Physiological Chemistry*, vol. ii., that it is by no means certain that *pure*, *strong* glycerine can dissolve any quantity of an enzyme. In most cases dilute glycerine is employed, the water (or dilute salt solution) being the active solvent. All enzymes are incapable of being dialysed, are carried down by fine precipitates of other substances in a purely mechanical manner, a property which is made use of in their artificial preparation, and when in solution all are destroyed by heat. Solutions of enzymes for the most part are at once rendered inactive by boiling; the highest temperature at which a ferment can exist and still retain its special properties is variously stated at 65°, 70°, and 80° C., though exposure to these temperatures for a prolonged period ultimately destroys them. Each ferment has an optimum temperature, at which its activity is greatest. Thus pepsin and the other ferments met with in the animal body act most strongly between 40° and 45° C. For diastase and malt ferment the best temperature lies between 60° and 65° C. (Chart I.) At the ordinary temperature of the air ferments are all capable of some degree of activity, while at 0° C. those of cold-blooded animals and plants, chiefly owing to their great concentration, possess powerful digestive properties. At the latter temperature the ferments of warm-blooded animals when in normal strength lose most of their activity, though they are not destroyed. On the other hand, experiments show that those of cold-blooded animals and plants, though sufficiently active at the ordinary temperature of the air or of water to do what is required of them, have their power greatly

increased at a higher temperature. If ferments be exposed in an absolutely dry condition to a temperature of even 150-160° C. their activity is not destroyed. Hüfner heated dry pancreas-ferment to 100° C.; Salkowski exposed dry pepsin to a temperature of 150° C. and invertin to 160° C.

CHART I.—Showing the effect of Temperature on the Activity of Salivary and Pancreatic Ferments (after Roberts).



for several hours at a time and found that they had lost none of their activity. All unformed ferments are precipitated from their solutions by alcohol, but their efficacy is not destroyed nor are they rendered insoluble in water or glycerine afterwards. In this they resemble native proteids such as albumin and globulin as well as the proteoses and

peptones derived from these bodies. Unorganised ferments, like most proteid bodies, are precipitated by saturation of their solutions with sulphate of ammonium. The precipitation of ferments by means of the addition of solutions of the heavy metals renders them inert. (Cf. Table XIII.)

TABLE XIII.—*Unorganised Ferments.*

Ferment.	Action on	Product.	Vegetable.	Animal.
1. Diastase	Starch	Maltose	In most plants	....
2. Do.	Inulin	Do.	Compositæ, etc.	....
3. Ptyalin	Starch	Maltose	....	In saliva
4. Amylopsin	Do.	Do.	....	Pancreatic juice
5. ?	Cellulose	Glucose	In seeds and tree fungi	....
6. ?	Do.	Marsh gas, acids, etc.	Bacteria	Bacteria in the intestine of herbivora
7. Invertin	Cane-sugar	Dextrose and lævulose	Fungi	....
8. Do.	Maltose	Do. do.	....	Intestinal glands
9. ?	Glycogen	Dextrose	....	In the liver?
10. Glucoside-splitting	Glucosides	Glucose, etc.	In plants	....
11. Steapsin	Neutral fats	Glycerine and fatty acids	....	Pancreatic juice
12. Similar body	Do.	Do.	In seeds	....
13. Proteolytic	Proteids	Peptones	Do.	In stomach and pancreas
a. Active in neutral solutions, papain	Proteids	Peptones	Fruit and seeds of some plants	....
b. Active in acid solutions, pepsin	Proteids	Peptones	In carnivorous plants	Gastric juice
c. Active in alkaline solutions, trypsin	Proteids	Peptones	....	Pancreatic juice
14. Rennet	Caseinogen	Casein and whey-albumose	Pinguicula, etc.	Stomach and pancreatic juice

A recent paper by Pekelharing (*Ztscht. f. phys. Chem.*, xxii. 2, s. 233) deals with a new method for the preparation of pure pepsin. The mucous membrane from ten pigs' stomachs is finely chopped up, and digested with six litres of a 0.5 per cent. solution of hydrochloric acid for five days at 37° Cent. The solution is then filtered and dialysed for 15 to 20 hours in running water. The contents of the dialyser are now filtered, the precipitate caught on a filter paper is dissolved in 0.2 per cent. hydrochloric acid and again dialysed as before. The precipitate which forms is collected on a filter paper, washed thoroughly with distilled water, and dried over sulphuric acid. Treatment of the original filtrate by concentration, addition of basic acetate of lead and ammonia, separation of the resulting precipitate by removal of the excess of lead with oxalic acid, and dialysis of the remaining substance, affords a precipitate identical with the first product obtained. The product, which possesses an extraordinarily great peptic power, dissolves with difficulty, when freshly made, in distilled water,

is much more soluble in weak salt solutions, and when dried forms a pale yellow powder with a slight power of absorbing water. Unfortunately Pekelharing was unable to procure a sufficient quantity of this pepsin to subject it to ultimate chemical analysis. He ascertained, however, that it gave the proteid reactions, contained phosphorus, and was split up, by heating in acid solutions, into a nucleo-proteid insoluble in acids, a substance containing phosphorus easily soluble in warm alcohol but with difficulty in cold, and into an albumose. If a solution of the pepsin was very gradually heated on a water bath this decomposition did not occur, but at the same time the pepsin lost its digestive power. It is possible that Pekelharing's product is absolutely pure pepsin free from foreign proteid bodies, and this view is supported by the fact that both the loss of peptic activity and the actual splitting up are caused by identical conditions. The statement made by many that, because an artificial gastric juice frequently fails to yield positive evidence of the presence of a proteid, pepsin cannot be of that nature, is shown by Pekelharing to be erroneous. His pepsin answered to all the proteid tests when in a concentrated solution, but when added to a dilute artificial gastric juice gave none of these reactions. The most striking and novel fact with regard to the pepsin thus obtained lies in the discovery of phosphorus compounds, which can be split off from it in the form of a nucleo-proteid, and an undetermined body as well as an albumose. As far as we know, no one before this has suggested that phosphorus is one of the elements of an unformed ferment either combined in the radical of nuclein or in another form. No chlorine is present, suggesting that the chlorine found by Schomnow and Simanowsky in their pepsin was derived from the hydrochloric acid of the gastric juice.

Hjört (*Centralbl. für Physiol.*, x. p. 192, 1896) has found that the juice of the majority of the higher fungi—*i.e.*, mushrooms, toadstools, etc.—possesses a proteolytic power resembling that of trypsin. Albumoses, peptone, and amido-acids can be obtained by its action upon albumin and globulin. The various forms of these fungi contain ferments which differ from each other in minor points.[1]

Zymogens.—The ferments which are secreted by the different glands engaged in the general process of digestion are not contained in the cells of the glands in a fully formed state. For example, the fresh pancreatic tissue may be free from any ready-formed proteolytic ferment, or may only contain traces of it. In a short time, a few hours, the pancreas after removal from the body always contains trypsin, and the time of its appearance may be hastened by treatment with dilute acids. Heidenhain, who first discovered this fact, called the forerunner

[1] In the acephalic mollusca (*Artemis exoleta*, etc.) Tiéri and Patier (*Arch. de Phys.*, 1897, No. 60) have demonstrated the presence of an oxidising ferment. It is only found in the tentacles, feelers, and blood, is soluble in water, and precipitated by alcohol. The ferment is most active at 60° C., and is destroyed at 100°; possesses most power in acid solutions, such as 0.2 to 0.3 per cent. acetic acid, little influence in neutral, and none in alkaline media.

of trypsin, *zymogen*. The term zymogen is now applied to the antecedents of the different unorganised ferments, so that Heidenhain's original zymogen may be termed the zymogen of trypsin, the others zymogens of their several ferments. Reasoning from analogy, we may confidently assert that all ferments are produced when required by the active cells of the different glands from an inactive precursor, formed by and present in these cells. On receipt of the proper stimulus the cells discharge their zymogens, which are probably converted into ferments or enzymes outside their walls.

The Secretion of Ferment-yielding Material—Ptyalinogen.—For some time after the discovery and identification of the zymogens of pepsin and trypsin the actual existence of a zymogen of ptyalin in the cells of the salivary glands could not be substantiated. Grützner thought that it was present in the saliva of the rabbit, and Goldschmidt, in an incomplete research, suggested its presence in that of the horse. Recently, Latimer and Warren have announced that it is present in many animals, especially in the rabbit, but absent in others, as for instance, in the sheep. They obtained the zymogen by extraction with chloroform water, in many cases after the action of very dilute acetic acid. The microscopic appearances of the secreting cells of the salivary glands differ very markedly in direct relationship to the activity of the cells examined. Mislawsky and Smirnow describe the cells of the parotid gland of the dog, when fasting, as having a single nucleus, protoplasm with fine granules, through which a delicate network could be descried, and a homogeneous ground substance. After section of the fibres of the sympathetic nerve and stimulation of the auriculo-temporal nerve, which conveys the nerve impulses from the brain to the gland, the granules become less in number, larger in size, vacuoles appear especially in the periphery of the cells, containing a slightly coloured substance and the remains of the network; while the nuclei become more distinct and larger. Fig. 32, on page 224, gives a representation of the nervous supply of the parotid gland. If, on the contrary, the auriculo-temporal nerve is cut and the sympathetic fibres stimulated, no flow of saliva occurs, the cells shrink, the network shrivels, the granules become small and numerous, and the nuclei increase in size. If the auriculo-temporal nerve is stimulated while the sympathetic fibres are intact, the granules completely disappear, large vacuoles fill the

cells, often leaving naught but the nucleus, and even that now and then vanishes, while Boll's star-shaped connective tissue cells become very prominent. During the disappearance of the granules, Langley observed that they gradually aggregated in the inner part of the cell, that is, the part next the lumen of the duct to which they were apposed. (Figs. 18 and 19.) The formation and extrusion of granules by the cells of the secretory glands are actions of the greatest importance, some indeed look upon these granules as actual zymogens, others are of opinion that the fully-formed enzyme is secreted by the cell. The furthest point to which it is safe to go in this matter is to state that the extrusion of granules by secretory cells implies a power of discharging protoplasmic products. That these products do contain a zymogen, in addition to other substances, is proved by the fact, ascertained by Goldschmidt, that the saliva of the horse does not become active if kept absolutely aseptic; the moment it becomes inoculated with an organised ferment, or micro-organism, as when it enters the mouth, the ptyalinogen which it must contain yields the ferment ptyalin, and the saliva immediately exhibits an amylolytic or starch-converting power.

Trypsinogen.—The cells of the pancreas exhibit very similar changes during activity. Heidenhain was able to differentiate between two zones in each cell, the outer easily stained, of a homogeneous character, and containing the nucleus; the inner, granular, staining with difficulty, and containing a fine network throughout its substance. The outer zone was regarded by Heidenhain as the protoplasmic, the inner as the "protoplasm-product" zone. In the fasting condition the inner and granular part occupies about two-thirds of the cell, the outer only about one-third; after activity the proportions are reversed, while the whole cell becomes smaller. Kühne and Lea have observed during life in the pancreas of the rabbit, which in that animal is scattered in isolated lobules between the layers of the mesentery, the actual process of secretion, and describe the gradual diminution in size of the inner zone, the aggregation of the granules towards the lumen of the tubule, their disappearance, and the increase of the protoplasmic, homogeneous zone as the granular one decreases. The whole process represents the flow of protoplasm and its products from the part of the cell nourished by the blood to the lumen of the tubule in whose walls the cell is placed. (Figs. 27 to 31.)

The pancreas when absolutely fresh contains no trypsin or only a trace of that ferment. If examined a few hours after removal from the body trypsin can always be detected. The conversion of the inactive zymogen into the active trypsin is connected with a change in the reaction of the gland tissue. After removal from the body the gland gradually becomes of acid reaction, and Heidenhain has proved that this acidity has to do with the conversion by showing that the addition of acids hastens the process. Trypsinogen is soluble in glycerine and in water, but splits up when dissolved in water, yielding trypsin, the rapidity of this action increasing with the temperature.

FIG. 27.

THE PANCREAS OF THE DOG WHEN INACTIVE DURING FASTING (IN SECTION).

(Meade Smith, after Heidenhain.)

The cells show two zones. The one next the lumen of the tubule clear and only slightly granular, the outer zone granular in appearance and containing the nucleus.

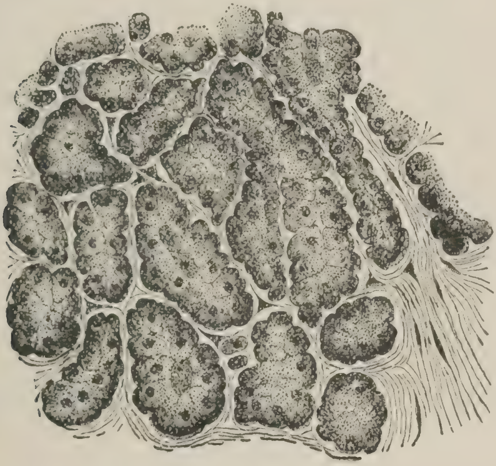
If the solution be acid in reaction the decomposition occurs more quickly. It can also take place in solutions of neutral and alkaline salts. In a fresh neutral solution of the pancreatic extract in glycerine trypsinogen appears to remain unaltered for an indefinite period. Kühne found that

alcohol causes the appearance of the actual ferment, and Podolinski (quoted by Heidenhain) has stated that the passage of oxygen through its solution sets trypsin free, although hydrogen has no such action. Peroxide of hydrogen and platinum black act similarly to oxygen. Trypsin can be extracted directly from the pancreas with glycerine if the gland is immersed for a short time in one per cent. acetic acid. As acids soon destroy the activity of trypsin the preliminary addition of acid must be of short duration.

Pepsinogen.—If a glycerine extract of the mucous membrane of the stomach be added to a solution of albumin and acidu-

FIG. 28.

THE PANCREAS OF THE DOG DURING THE FIRST STAGE OF ACTIVITY.



(Meade Smith, after Heidenhain.)

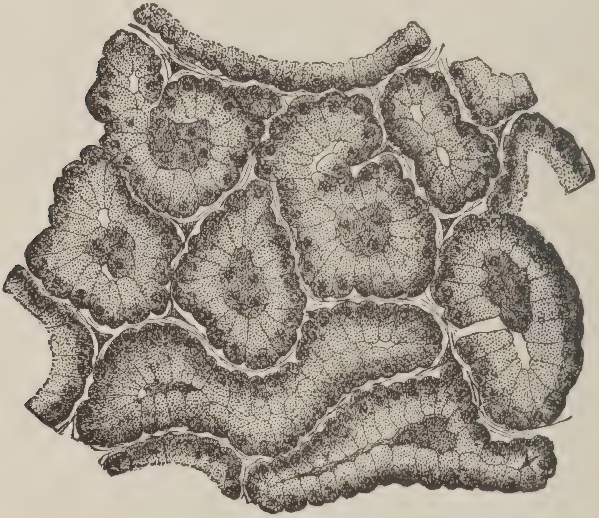
The zone next the lumen is now much more granular ; the zone further from it is narrower.

lated with hydrochloric acid, and if to another portion of the albumin solution the same amount of an extract, procured by the action of a dilute solution of hydrochloric acid on the gastric mucous membrane, be added, and the proportion of hydrochloric acid present rendered equal to that in the first specimen, it will be found that the glycerine extract contains a much less active ferment than the extract made by means of

the dilute acid. This difference occurs whether the mucous membrane of the fundus or of the pyloric region of the stomach is used for the extraction. Reasoning from this fact, Ebstein and Grützner assumed that the body removed from the gland cells could not be active pepsin, but a forerunner of that ferment which became active under the action of hydrochloric acid. This pro-pepsin, or pepsinogen, as it is called, was

FIG. 29.

THE PANCREAS OF THE DOG DURING THE SECOND STAGE OF ACTIVITY (IN SECTION).



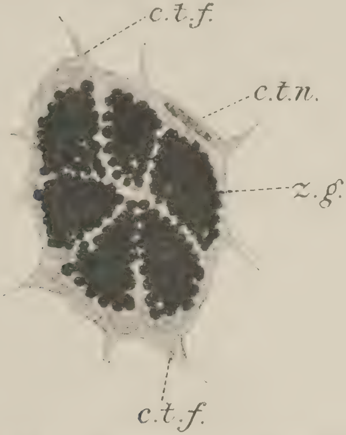
(Meade Smith, after Heidenhain.)

The cells are returning to the state present during fasting.

thought by them to be a combination of the ferment with the proteids of the gland cells. This suggestion, however, is rendered of doubtful value by the fact that glycerine is unable to extract all the pepsin from proteid bodies should they be contained in the same solution. Schiff found that an extract of the gastric mucous membrane, produced by means of acidulated water, increased in digestive power for some weeks. This, he thought, might be due to the presence of pro-pepsin, which

FIG. 30.

ACINUS OF THE PANCREAS OF THE TROUT IN THE RESTING STAGE.



(From a drawing by Dr. Lovell Gulland. × 1000.)

c.t.f. Connective tissue fibre; *c t.n.*, connective tissue nucleus; *z.g.*, zymogen granules.

FIG. 31.

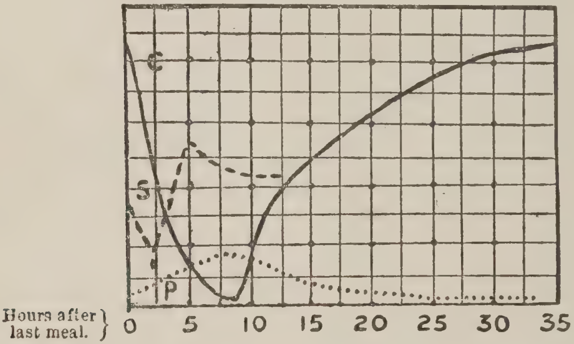
ACINUS OF THE PANCREAS OF THE TROUT IN THE ACTIVE STAGE.

(From a drawing by Dr. Lovell Gulland. × 1000.)

c.t f. Connective tissue fibre; *z.g.*, zymogen granules much diminished in number.

was only slowly converted into pepsin. Later evidence shows, however, that this body is converted into the ferment exceedingly rapidly in the presence of even very dilute hydrochloric acid. Although these observers suggested the probable existence of pepsinogen, Langley (*Journ. of Phys.*, vol. iii. p. 269) was the first to show conclusively that such a body exists. He found that pepsin, when digested at 40° C. with a .5 to 1 per cent. solution of sodium carbonate, is rapidly rendered inactive; pepsinogen, on the other hand, when similarly treated, is only

CHART II.—SECRETION OF PEPSIN.



C ———— Quantity of Pepsin in Mucous Membrane of the Cardiac end of the stomach after food.

P . . . . Pepsin in the Mucous Membrane of the Pyloric end.

S — — — — Quantity of Pepsin in the Secretion of the glands of the Cardiac region.

slowly affected. In the latter case the carbonate of sodium gradually produced small quantities of pepsin. Another fact which he adduced to prove the presence of this forerunner of the gastric ferment seems to be conclusive. If an active hydrochloric acid extract of the mucous membrane of the stomach be neutralised and treated with the solution of sodium carbonate mentioned above and then acidified again, it loses its peptic power, while a similar watery extract treated in the same way is still capable of proteolytic action on the addition

of acid. Langley concludes from his experiments that the gastric glands contain no active peptic ferment during life, but a quantity of zymogen, or forerunner of pepsin, and that this zymogen can be seen in the chief cells of the glands in the form of granules. During digestion the granules become used up, and under the microscope the outer zone of the chief cells becomes non-granular, the inner zone still containing these particles of zymogen. (Cf. Figs. 23-25.) Langley, working with Edkins (*loc. cit.*, vol. vii. p. 371), some time later published the results of further researches into these bodies. He found that pepsin was readily destroyed by alkalies, and even to a considerable extent on neutralisation of its acid solution. Pepsinogen is similarly affected, but its destruction is very much slower. All the pepsinogen present in an aqueous extract of the stomach of a cat was converted into pepsin in sixty seconds by the addition of a 1 per cent. solution of hydrochloric acid. Carbonic acid, when passed through a solution of pepsinogen in water, destroys a large portion of it, and this more rapidly than pepsin. The presence of peptone and other proteids delays the rate of destruction by carbonic acid; certain salts increase the rate. (Chart II.)

Rennet-zymogen.—Only from the fresh gastric mucous membrane of the calf and of the sheep can the fully-formed active rennet or milk-curdling ferment be extracted by means of water or other similar solvents. As a rule no substance capable of curdling milk can be obtained by treatment with water from the mucous membrane of the stomach of other members of the *Mammalia* or of *Aves*. It is almost never present in fish. If, however, acid be added to the watery solution, the zymogen quickly yields the true ferment. The variations in the amount of rennet-zymogen in the gastric mucous membrane correspond very closely to those of pepsinogen. As is the case in other zymogens, a more active extract of the rennet-zymogen can be obtained by the use of an acid solution. The extracts procured from the calf and sheep by water alone do not exhibit nearly so powerful an action as those obtained by acidulated solutions.

It is possible that a zymogen of the pancreatic amylolytic ferment exists in the pancreatic cells, but if so it must, unlike the zymogens of pepsin and trypsin, be insoluble in water. Liversidge removed all the diastatic ferment present in the minced pancreas with long-continued washing with water until no more could be obtained; on exposing the gland to the air for a few hours, however, a fresh quantity of very active ferment could be extracted with distilled water. It is possible that all bacterial action was not provided against, but allowing for this, it appears to be logical, even in the absence of further proof, to postulate the presence of such a zymogen, especially as the other ferments in the body are preceded by these bodies.

The maltose inverting ferment of the intestinal mucous membrane also is probably preceded by a zymogen.

As all ferments are the products of cell-protoplasm, it is only natural to conceive that the cells especially set apart for the elaboration of these bodies should in the intervals of rest form and store up substances which can be converted into active ferments in the shortest time possible. And also that they should store them up in an inert and innocuous form corresponding to the zymogens which have already been discovered. Protoplasm itself is a zymogen, and the zymogens of the digestive ferments constitute a moiety of the total fermentative properties of protoplasmic action, split off for greater ease in distribution and for the relief of the protoplasm left, which, like a thrifty housewife with her savings in the bank, proceeds to hoard up more to add to the "running account."

The formation of zymogens, then, appears to serve the purpose of providing an already prepared store of ferment material, only requiring the necessary stimulus derived directly or indirectly from the food to be discharged into a medium capable of converting them into active agents, while their separation in the form of granules from the general mass of cell protoplasm allows of its recuperation even before the products of its energy have been expelled.

Glucoside-splitting Ferments.—Another class of ferments which exist in a small number of plants has the power of splitting up glucosides into glucose and other bodies. Examples of these are myrosin, from *sinapis*, and emulsin from *amygdala*. Myrosin has as yet never been obtained free from albumin or lime: its solution froths on shaking, and coagulates at 60° C. and on the addition of acids and alcohol. If a small quantity of this substance be added to a solution of myronate of potash, a compound present in mustard seeds belonging to the class of glucosides, volatile oil of mustard is formed, along with glucose and bisulphate of potash. The myrosin, like most other unorganised ferments, does not enter physically into the reaction, it only helps the glucoside to split up into simpler compounds, thus—

$$C_{10}H_{18}K.NS_2O_{10} = C_4H_5NS + C_6H_{12}O_6 + HKSO_4.$$

This reaction only occurs in the presence of water. The volatile oil thus formed gives to mustard its irritating qualities. Emulsin acts similarly on the glucoside, amygdalin, of the

bitter almond, splitting it in the presence of water into glucose, the essential oil, and hydrocyanic acid, thus—

$$C_{20}H_{27}NO_{11} + 2H_2O = C_6H_5COH + HCN + 2C_6H_{12}O_6.$$

Sigmund (*Monatshefte für Chemie*, xiii., 1892) has found that the glucoside-splitting ferments are closely connected with the fat-splitting ferments. The fat-splitting ferments can act on glucosides and on ethers and esters; the glucoside-splitting ferments on fats and ethers. Fischer (*Bericht d. d. Chem. Ges.*, xxvii. 2, 2031) states that invertin from beer-yeast acts on various glucosides of the α class, while emulsin split up the isomeric β-glucosides.

THE ORGANISED FERMENTS.

The term organised or formed ferments is applied to those minute vegetable bodies, the moulds, yeasts, and bacteria, by whose growth changes are brought about in the constituents of the media nourishing them, analogous to the chemical phenomena resulting from the action of the unformed ferments. The action of the formed ferment differs from that of the unformed in that it is infinite not finite, and in that the changes brought about are accessory to, and greatly in excess of, the needs of the active agent. The action of an unformed ferment is finite; a certain quantity is capable of chemically transforming a proportionally large but still only a definite amount of material; the action of a formed ferment is infinite in so far that however large in amount the soil may be, provided the conditions remain suitable, the smallest quantity capable of growth suffices to act on the whole soil, while a portion removed from the first growth is just as capable of complete action on a second supply of the medium. In short, the one has the attributes attendant on living matter, the other only those appertaining to inanimate bodies.

A number of properties are common to the formed and unformed ferments, while the points of difference between them in regard to their actions are few in number and indefinite in character.

TABLE XIV.—*To show the points of Similarity and Dissimilarity between Unorganised Ferments, Organised Ferments, and Proteids.*

	Unorganised Ferments.	Organised Ferments.	Proteids.
Temperature— In solution, 65° C. to 80° C.	Destroyed.	Destroyed except some with spores.	Native proteids coagulated, derivative proteids unchanged.
In a dry state, 100° C. to 160° C.	Many unchanged.	All killed in a few hours.	Albumins and Globulins altered in time.
Alcohol.	Precipitated, still active, activity diminishes in time.	Killed.	Precipitated, and in time, if in native form, coagulated.
Antiseptics.	Unaltered if solution be dilute.	Killed.	Various.

That the points of difference between the two classes of ferments should be small is not surprising if it be remembered that the one arises from the action of the protoplasm of single living cells immersed in the substance on which they grow, while the other is the product of cells fixed in body tissues, capable of further production, but incapable of actual multiplication of productive cells. Formed ferments are organised protoplasmic cells with an infinite power of expansion under favourable circumstances, producing chemical changes of a similar character to those brought about by the protoplasmic activity of cells which form part of a composite organism, and are specialised for the purpose of secreting unformed ferments or enzymes. Both are similar in that they are destroyed by heating to the boiling point of water when in suspension or in solution in fluids, although the unformed are less resistant to the action of heat than the formed ferments, as the latter are in part protected by their cellulose coating. When dry either class can withstand, as a general rule, a higher temperature for a limited time without loss of function. Neither can act in the absence of water, while if the solutions containing them be saturated with neutral salts the formed ferments are rendered absolutely inactive, and the unformed ferments checked, or, as in the case of trypsin (Neumeister), rendered almost inert. Perhaps one of the most striking similarities between the formed and unformed ferments is the coincidence in the

maximum temperature at which they are most active. The temperature of the body appears to afford most ferments the greatest possible facility for the fulfilment of their functions; they are able to act in higher and in lower temperatures, but not so powerfully. The formed ferments are checked and in a few cases destroyed by a temperature of or below the freezing point of water; a similar temperature slows the action of the unformed ferments, although their activity may often, as in the cold-blooded animals, appear to be as great as when the temperature is higher. The reason of this apparent contradiction has been shown to be due to the large amount of the ferments present, the increased bulk equalising the lessened power (cf. p. 253).

The interesting observation was made by Paul Bert, that the formed ferments are killed if subjected to the action of oxygen under the compression of many atmospheres; the unformed ferments are unaltered. Pasteur, however, found that the spores of certain formed fermentative agents can resist a pressure of from ten to twelve atmospheres. All these facts go to show that the rationale of the fermentative processes initiated by organised agents is only divided by a very narrow line from that which underlies the chemical changes initiated by the unorganised class.

Two further examples may be given of the similarity between them. Lechartier and Bellamy found that when chopped up leaves and fruits of phanerogams were placed in an atmosphere devoid of oxygen, as in carbonic acid, they developed alcohol from the carbo-hydrates present, in the total absence of yeast; an observation which confirms a previous statement of Pasteur. This production of alcohol seems to be one of the stages which occur in all plants during the intra-molecular conversion of starch into carbonic acid and water. The sudden deprivation of the oxygen necessary to further convert the alcohol into these end-products acts, as Ewald says, as a surprise to the intra-molecular respiration, which, in lieu of oxygen, exhausts the requisite elements present in the cells, but can proceed no further for lack of the oxygen. Those who believe in the doctrine of the chemical nature of all fermentation regard this intra-molecular respiration as due to a special unorganised ferment present in the cell, akin to Traube's hypothetical alcoholic ferment in yeast.

A second example is given by the self-fermentation of yeasts, by which they are able, in the absence of sugar, under certain conditions, to produce alcohol and sugar from their own substance. Bechamp and Schutzenberger suggest that in a similar way products of the fermentation of nitrogenous bodies, such as leucin, tyrosin, etc., can be formed from yeast-cells, although Naegeli's explanation is more feasible when he states that such profound chemical alterations are due to bacteria growing at the expense of the decaying yeast-cells.

These observations apparently support the view that all fermentative processes, the chief result of which is the simplification and oxidation of complex molecules, are initiated by chemical substances formed by protoplasmic activity. The objection that has been urged against this application of Lechartier and Bellamy's observation—viz., that destruction of yeast by the addition of alcohol, or arrest of its activity by deprivation of oxygen, inhibits the fermentation, while unorganised ferments are independent of the presence of that element—may be met by the fact that the quantity of unorganised ferment produced by the yeast-cells is probably very small relatively to the amount of sugar present, and is used up in great part shortly after production in the fermentative processes which it causes. As has already been stated, a gradual fermentative action has been observed after the death of the cells, an action which is gradual because of the small amount of ferment present.

Products of the Activity of Formed Ferments.—Starch is not produced as a rule by any of the fungi. From Naegeli's observations the lower fungi can form fat from carbo-hydrates in the same way as fats are produced from starch and sugars in ripening seeds; these fungi, however, are able to form fat from proteids and other nitrogenous organic compounds. Moulds and yeasts placed in distilled water form a certain amount of fat at the expense of their proteid substance. Bacteria flourish in a solution of proteid material, and increasing in number cause an increase of fat, it may be to more than a millionfold; and when grown in solutions containing little proteid but much sugar or tartaric acid, the increase of albumin is derived from the nitrogenous, while most of the fat and cellulose produced comes from the non-nitrogenous, compounds present. For the formation of fat free oxygen must be obtainable; the moulds only grow when they have access to free oxygen, and they abound in fat; the yeasts and bacteria require little oxygen and are correspondingly deficient in this substance. Those portions of mould-fungi growing on the surface of a solution contain more fat than the portions submerged, and their resting spores only yield much fat when developed on hyphæ which reach up into the air. The formed ferments are thus able to form fat from both nitrogenous and non-nitrogenous compounds, but apparently only in the presence of oxygen. They produce no starch, little if any true sugar, are often able to manufacture mannite (cf. p. 140), and can form a cellulose different from that in other plants in that it does not give a blue colour with iodine and sulphuric acid; indeed Winterstein suggests that fungus-cellulose is not

a simple molecule of the composition $C_6H_{10}O_5$, but a compound of this and a molecule of a nitrogenous substance.

Unformed Ferments produced by Fungi.—Yeast-cells form a ferment called *invertin* which passes out into the solution round about them. Invertin splits up cane-sugar into dextrose and lævulose, forms which can be acted on by the yeast-cells with the production of alcohol. If sufficient chloroform be now added to kill the cells the solution can still act on cane-sugar in virtue of the invertin present in it, but no further conversion of dextrose into alcohol occurs owing to the death of the cells.

If a watery solution containing shreds of fresh fibrin from blood be left for some weeks exposed to the air, especially if at a temperature of about 38° C., the fibrin gradually dissolves, foul gases are evolved, and in time, should the supply of oxygen be sufficient, the complex proteid molecules are reduced to the end-products carbonic acid, water, ammonia, and sulphuric acid, apart from the portions taken up in the formation of the protoplasm and cellulose of new bacteria. If such a mixture of fibrin and water be exposed to the air for a shorter period and chloroform water then added to it, a similar dissolution of the fibrin occurs unaccompanied by the production of gas and terminating in the formation of proteid derivatives. In this case the action is carried on by the small quantity of unformed ferment produced by the bacteria before death and unaffected by the chloroform water. Salkowski first described this experiment in 1889, but later investigations have shown the possibility of a fallacy occurring through the use of chloroform water, as some observers have found that the continued action of chloroform on proteids results in an appreciable conversion of these bodies into peptones. The employment of a saturated solution of potassium nitrate in place of the chloroform water by Limbourg has, however, shown the result to be correct, as peptonisation continues in such a solution although the growth of the bacteria is completely arrested.

The two instances just given are examples of formed ferments producing diffusible unformed ferments capable of acting outside the cell. Many other bacteria produce similar ferments which only act intra-cellularly on simple and easily diffusible food-stuffs penetrating their outer covering.

All substances which coagulate or precipitate native albumins

and globulins by so doing arrest the action of the formed ferments. If, however, the solution in which the micro-organisms are growing be highly albuminous, combinations between the proteids and the precipitant fall to the bottom of the fluid and may free the solution from the poisonous substance in an active state, and still allow the growth of bacteria to continue, provided the substance added be not in excess of the combining power of the proteids. In such an instance a quantity of corrosive sublimate may be added without arresting all ferment action which would be quite sufficient to check all growth in a non-albuminous solution of the same bulk. On the other hand, the unformed ferments, although their activity may be diminished in the presence of such protoplasmic poisons as alcohol, ether, chloroform, thymol, etc., on their removal or dilution recover their former power. All mineral-acids in solutions of above 0.2 per cent. destroy sooner or later both the unformed and the formed ferments, with the remarkable exception of pepsin. It does not follow from this that all the formed ferments are unable to flourish in an acid medium provided it be of a lower strength, for many bacteria and yeasts appear to favour a slight acidity—indeed many form acids by their action, acids which in time, should they pass a certain degree of strength, exert an inhibitory effect on the organisms producing them. Similarly many of the enzymes or unformed ferments which are destroyed in time by very weak acid solutions are capable of energetic action in the very medium which will later on cause their destruction.

A similar arrest of activity in the formed ferments to that occurring by reason of the acid they produce is brought about by the accumulation of many other of their products; the growth of the yeast is in time checked by the alcohol it forms from sugar; the organisms of putrefaction cease multiplying when the phenol, or carbolic acid, they form reaches the concentration inimical to them, an interesting example of Nature's application for antiseptic purposes of the substance which was the first to be used by man in his recent departure in treatment, when he unwittingly employed a body formed by bacteria as a check to their growth, and as an agent for their destruction.

The unformed ferments are also arrested by an accumulation of the products of their activity, although here again we find an exception, as the milk-curdling ferment or rennet does

not appear to lose any of its efficacy however great the accumulation of casein coagulated by it may be.

Both classes of ferments possess the property of splitting peroxide of hydrogen (H_2O_2) into water and oxygen when placed in its solution. Jacobsen (*Ueber Ungeformte Fermente*, Inaug. Diss., Berlin, 1891) found, however, that the ferments of the pancreatic juice when heated to 60° C., and allowed to cool down to 40°, lost the power of decomposing peroxide of hydrogen, although they still retained an unimpaired diastatic action. Precipitation of the unformed ferments by saturation of their solutions with neutral salts, or by the addition of alcohol in excess, renders them incapable of acting on peroxide of hydrogen, although they are still able to produce their special changes on food-stuffs. The property of decomposing peroxide of hydrogen belonging to the unformed ferments is therefore independent of their digestive action. Probably the products of the formed ferments would be found on investigation to contain unformed ferments responding in like manner.

TABLE XV.—*The Chronology of Ferment Action.*

1833 .. ..Payen and Persoz : On diastase.
1838 ....Cagniard-Latour : Vinous fermentation.
Schwann : Alcoholic fermentation and putrefaction.
Berzelius : Action by catalysis, digestion caused by contact with ferments which are bodies capable of initiating chemical changes without loss or alteration of their own structure.
1840 ....Liebig modified this catalytic theory, supposing that the ferment is a body in a state analogous to decomposition, its own changes starting those in other bodies.
1870 *et seq.* ...Pasteur lays down the law that there are two forms of ferments :—
(1) Organised, or capable of reproduction, fermentation being due to its living action.
(2) Unorganised, incapable of reproduction, action due to chemical change.
Present day...The first class, as described by Pasteur, is recognised to act as he suggested.
The second class is looked upon as consisting of complex chemical bodies of unstable composition, contact with which, in the presence of an active agent such as an acid or alkali, causes a splitting or an isomeric change in the size of the molecules of the substance acted on, usually accompanied with hydration.

CHAPTER VI.

FOOD ELEMENTS.

CARBO-HYDRATES :— Composition — Polysaccharides — Disaccharides — Monosaccharides.
PROTEIDS :—Composition—Properties—Classification—Scheme of Proteid Decomposition.
FATS :—Composition—Properties.

CARBO-HYDRATES.

THE carbo-hydrates are bodies containing three elements, carbon, hydrogen, and oxygen, the latter two in the exact proportions necessary to form water. A carbo-hydrate molecule may be formed by varying numbers of carbon atoms, and of atoms of the other two elements, but two hydrogen atoms are always present for each atom of oxygen. This characteristic is not confined to the carbo-hydrate group; acetic acid, for instance, $C_2H_4O_2$, shows the same proportion of hydrogen to oxygen atoms. In almost all the members of the carbo-hydrate group, however, the atoms of carbon in each molecule number six or multiples of six. The exceptions, the trioses, tetroses, pentoses, octoses, and nonoses, are of little importance with reference to nutrition.

The carbo-hydrates are divided into three classes—

1. Polysaccharides.
2. Disaccharides.
3. Monosaccharides.

The polysaccharide molecule may be regarded as a multiple of the monosaccharide molecule *minus* the elements of water, or conversely the monosaccharide as a part of the polysaccharide molecule *plus* water. The disaccharides are equal to two monosaccharide molecules *minus* a molecule of water.

The formulæ for these groups are :—

Polysaccharides ......$(C_6 18_{10} O_5)x = (C_6H_{12}O_6 - H_2O)x$
Disaccharides ....$C_{12}H_{22}O_{11} = (C_6H_{12}O_6 + C_6H_{12}O_6 - H_2O)$
Monosaccharides ...$C_6H_{12}O$

The Polysaccharides (Saccharo-Colloids, Amyloses).

The members of this group are made up, as we have seen, of multiples of the molecule of the monosaccharides with the subtraction of water. Sabanejeff (*Chem. Centralblatt*, 1891, s. 10) estimated the molecular weight of glycogen to be 1625. If the figure 10 be substituted for the sign x in the formula given above, a molecular weight of 1620 is obtained, agreeing very closely with the physical result.

$$^{1}\ (C_6H_{10}O_5)10 = (12 \times 6 + 1 \times 10 + 16 \times 5)10$$
$$= (162)_{10} = 1620.$$

Brown and Heron double the constituent atoms, and regard a molecule of starch as represented by $(C_{12}H_{20}O_{10})10$, with a molecular weight of 3240.

The principal polysaccharides are—

- Vegetable starch.
- Animal starch (glycogen). (In the liver and other animal tissues.)
- Dextrins. (Exemplified in toasted bread.)
- Cellulose. (The principal constituent of woody fibre, cotton wool, etc.)
- Reserve cellulose.
- Gums.
- Inulin.

The polysaccharides are all tasteless, amorphous, more or less soluble in water, except cellulose which is absolutely insoluble, and are insoluble in alcohol and ether. Starch and glycogen form opalescent solutions in water. All of them when dissolved in water are optically active, and are indiffusible through dialysing parchment. Saturation of their solutions with salts, especially with ammonium sulphate, causes their precipitation. They form no compounds with bases or with phenyl-hydrazin, nor do they reduce alkaline solutions of copper salts, except after long-continued boiling. If the polysaccharides be subjected to the action of steam at high pressure, of boiling in dilute mineral acid solutions, or of ferments, they are converted through the stages represented by dextrins and disaccharides into monosaccharides.

[1] In chemistry, the atomic weight of carbon is given approximately as 12, of hydrogen as 1, and of oxygen as 16. The sum of the number of atoms of each element multiplied by their atomic weights yields the relative molecular weight.

Thus starch is finally converted into glucose, after passing through the different kinds of dextrin, and the form of maltose. Glycogen and cellulose are also split up into glucose, inulin into lævulose, reserve-cellulose into mannose, and gums into galactose. The dextrins differ from the other members of the group, and indeed may be looked upon as forming a connecting chain, made up of bodies with progressively smaller molecules, between the polysaccharides and the disaccharides. They are easily soluble in water and are diffusible, slightly only when akin to the polysaccharides, freely when approaching to the constitution of the disaccharides. Starch subjected to a high temperature, but below the point of incineration, changes into dextrins, as exemplified every day in bread-crust or toasted bread.

The Disaccharides (Hexobioses, Sucroses).

The Disaccharides comprise:—

Cane-sugar (sucrose or saccharose).
Milk sugar (lactose).
Malt sugar (maltose, ptyalose).
Cane-sugar = 1 molecule of dextrose and 1 molecule of lævulose (*minus* 1 molecule of water).
Milk sugar = 1 molecule of dextrose and 1 molecule of galactose (*minus* 1 molecule of water).
Malt sugar = 2 molecules of dextrose (*minus* 1 molecule of water).

These sugars are soluble in water and alcohol, are optically active, crystallise, are capable of diffusion, and have a sweet taste, sweeter than the monosaccharides. They form compounds with bases; hydrazones and ozazones with phenylhydrazin. When dry they form caramel on the application of heat. With the noteworthy exception of cane-sugar they reduce metallic oxides in alkaline solutions.

Steam at high pressure, boiling with dilute mineral acids and inverting ferments, convert them into monosaccharides. The sucroses do not readily undergo fermentation until converted into glucoses. Bacteria help in this action by secreting an inverting ferment. A peculiar sugar, raffinose, is known, with a molecule made up of a combination of dextrose, lævulose, and galactose, thus being a trisaccharide or hexotriose ($C_{18}H_{32}O_{16}$). It occurs in barley, in eucalyptus-manna, and in the seeds of the cotton plant.

Monosaccharides (Glucoses or Hexoses).

1. Grape-sugar, glucose or dextrose.
2. Fruit-sugar, lævulose or fructose.
3. Mannose.
4. Galactose (distinct from lactose).

All these sugars have the same chemical composition; that is, they are isomers of each other, but three are simple isomers; their molecular grouping is the same, but the arrangement of the groups of atoms is different; while one, lævulose, is a stereoïsomer, the position of the atom-groups to one another not being the same.

Dextrose, mannose, and galactose are supposed to be made up thus (Neumeister)—

$$CH_2.OH - (CH.OH)_4 - C\genfrac{}{}{0pt}{}{H}{O} = C_6H_{12}O_6;$$

while lævulose is represented as—

$$CH_2.OH - (CH.OH)_3 - CO - CH_2.OH = C_6H_{12}O_6.$$

They are actually oxidation products of stereoïsomeric hex-acid alcohols, $C_6H_{14}O_6$; or

$$CH_2.OH - (CH.OH)_4 - CH_2.OH,$$

of which three are known to occur in nature, sorbite, mannite, and dulcite. Sorbite is obtained from the berries of the mountain ash, *Sorbus aucuparius*, mannite from the manna of *Fraxinus ornus*, and dulcite from Madagascar manna, in *Euonymus Europæus*, etc.

Dextrose, mannose, and galactose are the aldehydes of sorbite, mannite, and dulcite respectively, while lævulose is the ketose of mannite.

The glucoses are easily acted upon by organisms; many yeasts form alcohol and carbonic acid from them:

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} = \underset{\text{Ethyl alcohol.}}{2C_2H_5.OH} + \underset{\text{Carbonic acid.}}{2CO_2.}$$

Other organisms form lactic acid:

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} = \underset{\text{Lactic acid.}}{2(CH_3 - CH.OH - COOH)} \text{ or } 2C_3H_6O_3.$$

Like aldehydes and ketones, all the glucoses can form hydrazones and ozazones from hydrazins. Fischer has by careful oxidation of the hexyl-alcohols succeeded in obtaining mannose and lævulose from mannite, and has also built up synthetically the simpler sugars from elementary carbon compounds. The far-reaching significance of the work of this German chemist on the relationship between the different sugars and their synthetic preparation can hardly be over-estimated, but an investigation into his

results to be of value would require to be exhaustive, and therefore out of place here. It must suffice to state that true mannose can be formed from chemically made akrose, by way of akrit, a hexyl-alcohol, identical with inactive mannite, and of inactive mannose, finally forming true mannose, capable of rotating the plane of polarised light to the right; that the splitting up of the ozazone of this mannose affords lævulose, rotating polarised light to the left; and that by acting on the synthetic, as well as the natural, mannose with bromine water, the corresponding mannonic acid can be obtained, and from it glycuronic acid, which when reduced by nascent oxygen yields a glucose not to be distinguished from natural grape-sugar. A great number of these isomeric sugars are theoretically possible, and a considerable number have been isolated, as sorbinose, rhamnose, arabinose, etc.[1] A substance of great interest, amido-glucose, or glucosamine, contains nitrogen, one atom of amidogen replacing one of hydrogen in the glucose molecule. This body can be obtained from the proteid bodies chitin and chondroitin, and affords glucose when treated with nitrous acid.

$$\underset{\text{Glucosamine.}}{C_6H_{11}O_5.NH_2} + \underset{\text{Nitrous acid.}}{NOOH} = \underset{\text{Glucose.}}{C_6H_{12}O_6} + \underset{\text{Nitrogen.}}{N_2} + \underset{\text{Water.}}{H_2O}$$

PROTEIDS.

The most important rôle in the play of life is undoubtedly that acted by the group of complex chemical bodies bearing the name of proteids. No living cell in either the animal or the vegetable world but plays its part in the drama by means of proteids endowed with that mysterious force "vitality." A proteid body by itself is incapable of reproducing its kind, but as the chief constituent of living protoplasm it is, as it were, touched by a magician's wand, and enabled to perform the many different processes which are requisite for the production of the body and framework of each being, for its nourishment, and for the continuance of its kind. Protoplasm indeed is maintained by some to be only "living proteid," the change from life to death to be only a molecular one. But such a hypothesis is untenable. Protoplasm consists of the three classes of bodies used in alimentation with, in addition, a varying amount of mineral matter.

[1] A sugar—pentose—has been obtained from different members of the nucleo-albumin group of proteids by Blumenthal, who has separated this carbo-hydrate from the nucleo-albumin of the pancreas, liver, thymus, thyroid, spleen, brain, and muscles. Pentose molecules consist of condensed molecules of hexose bodies, where all or part of the aldehyde groups are shielded from oxidation by condensation, as for example in hemicellulose and cellulose. These arise by oxidation, and by splitting off, from the final alcohol groups of glucose and galactose molecules undergoing disintegration. (Chalmot, *Ber. d. d. Chem. Ges.*, xxvii. s. 2722.)

Chiefly made up of proteid, it probably contains some carbo-hydrate and fatty bodies either in close conjunction or in actual conjunction with the proteid, forming exceedingly complex molecules ready to give off various combinations of their atoms when called upon by the needs of the organism of which they form a part. It is one of the most suggestive things possible to watch the movements of the protoplasmic contents in the single cell of the *Vampyrella spirogyræ*, a microscopic, almost naked mass of protoplasm, and to observe the manner in which it exercises a power of discretion as to what food it should engulf in its substance, and what it should reject, and to think that when devoid of life this simple mass of protoplasm consists only of a minute speck of proteid and carbo-hydrate molecules, with purely chemical attributes. Well might Cienkowski exclaim after watching this phenomenon, "The behaviour of these monads in the search for, and ingestion of, their food is so remarkable that the observer might almost believe their actions to be those of a conscious being."

TABLE XVI.—*The Proteids.*

I.—*Animal (partly after Hoppe-Seyler.)*

I. Albumins: *a.* Serum-albumin; *b.* Lact-albumin; *c.* Egg-albumin.
II. Globulins: A. Precipitated by saturation with NaCl.
a. Myosin; *b.* Fibrinogen; *c.* Fibrin-globulin; *d.* Serum-globulin.
B. Not precipitated by saturation with NaCl.
a. Vitellin; *b.* Globulin from the Crystalline Lens (Crystallin).
III. Fibrin.
IV. Coagulated Albumins and Globulins.
V. Amyloid.
VI. Acid-albumin or Syntonin.
VII. Alkali-albumins, Albuminates, or Albuminic Acids.
VIII. Nucleo-albumins: *a.* Nucleo-albumin in Cell Nuclei; *b.* Vitellin; *c.* Casein; *d.* Spermatin.
IX. Mucin from Gall-bladder (probably a Nucleo-albumin).
X. Albumoses: A. Insoluble in water.
a. Hetero-albumose; *b.* Dys-albumose; *c.* Anti-albumid.
B. Soluble in water.
a. Proto-albumose; *b.* Deutero-albumose; *c.* Atmid-albumin; *d.* Atmid-albumose.
XI. Peptones: *a.* Ampho- or Hemi-peptone; *b.* Anti-peptone.
XII. Oxyproto-sulphonic Acid.

XIII. Albuminoids: A. *In Vertebrata*— *a.* Keratins, Neuro-keratin.
b. Elastins.
c. Collagen, Gelatins.

B. *In Invertebrata*— *a.* Conchiolin, *b.* Spongin, *c.* Chitin, *d.* Cornein, *e.* Fibroin, *f.* Silk — Skeletins (Krukenberg).

C. *Glucosides*— *a.* Mucin.
(*b.* Chitin)
c. Chondroitic Acid.

II.—*Vegetable.*

I. Vegetable Albumins.
II. Globulins: *a.* Vegetable Myosin; *b.* Vegetable Vitellin (Phyto-vitellin); *c.* Para-globulin.
III. Coagulated Proteids: *a.* Coagulated by heat;
b. By ferment action—1. Gluten.
2. Anti-vitellid, etc.
IV. Acid and Alkali Albuminates: *a.* Legumin or Vegetable Casein;
b. Conglutin.
V. Albumoses: *a.* α-phyt-albumose (Proto-albumose?);
b. β-phyt-albumose (Hetero-albumose?);
c. Insoluble Phyt-albumose (Dys-albumose?);
d. Vitelloses.
VI. Peptones.

III.—*Pigments of a composition similar to or combined with Proteids.*

A. Animal—

I. Hæmoglobin: Albumin and Hæmatin; Hæmocyanin, Histo-hæmatins.
II. Melanins.
III. Chlorophyll.
IV. Lipochromes.
V. Bilirubin, etc., in Bile.

B. Vegetable—

I. Chlorophyll.
II. Xanthic Series.
III. Cyanic Series.
IV. Lipochromes.

The class of proteids is a large one, but all the members present certain features in common. First, they may be separated into two broad groups—those which occur as part of the living tissues and fluids on plants and animals, and those which can be derived from the first group by various means. The first class are termed native, the second derived proteids. All proteid substances contain the five elements, carbon, hydrogen, nitrogen, sulphur, and oxygen. The exact composition of all the varieties is still uncertain. Proteids are so easily altered in constitution by any of the methods requisite for their isolation, and have so great an affinity for so many chemical substances, that,

hitherto, the analyses performed by even the ablest chemists present results which vary within considerable limits. The following figures give the different values obtained by various investigators, with the mean which may be regarded as the approximate constitution of the proteid molecule :—

Carbon	......50-55 per cent.	Mean	52 per cent.
Hydrogen	...6.5-7.3 ,,	,,	7 ,,
Nitrogen	...15-17.5 ,,	,,	16 ,,
Sulphur	......0.3-2.4 ,,	,,	2 ,,
Oxygen	......19-24 ,,	,,	23 ,,

Other elements are present in some proteid bodies, but only in small quantities, as for instance, iron in hæmatin, and phosphorus in the group of nucleo-proteids. Two atoms of sulphur are present at the least in each molecule, for if albumin be heated with a dilute solution of potassium hydrate, part of the sulphur forms a sulphate, and can be precipitated and removed by the addition of acetate of lead, leaving a part, probably united with other substances, in the original molecule, and that more firmly fixed, though it can be transformed easily into sulphuric acid by heating with the hydrate and nitrate of potassium. In the same way, part of the nitrogen of the proteid molecule, when heated with a weak solution of potassium hydrate, forms ammonia and is driven off, the larger portion remaining in the solution. It is plain, therefore, that we have to deal with a very complicated molecule in which the various atoms are united to one another with different degrees of force, while in all probability the whole molecule is made up of congeries of atoms, each a molecule in itself, which are prone to separate from the parent molecule on receipt of the proper stimulus. The typical proteid molecule, then, is a large, unstable composite body, and there is reason to believe that, as we have seen when discussing the molecule of starch, several of these compound molecules are combined together in native proteids to form a still larger, doubly-compound body. It is only on this supposition that the formation of differently constituted substances from albumin during digestion, with at the same time the continued presence of proteid bodies with practically the same composition per cent., though with other physical qualities, can be satisfactorily explained in the present state of our knowledge.

In addition to the elements described above as entering into the composition of the proteid molecule, we must not forget to

add that the native proteids are looked upon as being in a state of low hydration, that is, they have very few molecules of water attached to them in their natural condition. Indeed, the alteration in their characteristics, brought about by digestion, or by similar artificial means, is to be regarded mainly as a splitting up and cleavage of the compound molecules accompanied by the addition of the elements of water. The lower we go in the proteid scale the larger we find the proportion of water connected with the typical proteid molecule to be All proteids are insoluble in alcohol, and all are precipitated from their solutions by it; although only the native proteids become coagulated by the prolonged action of alcohol and are then insoluble in water; the derived proteids can always be redissolved, however long they may be exposed to its action. All proteids are precipitated by soluble salts of the heavy metals, but can be separated from the metallic combinations thus formed by appropriate means. They are also precipitated by potassio-mercuric iodide and hydrochloric acid, by picric acid (derived proteids are soluble on heating with this acid, though re-precipitated on cooling), by Millon's reagent with the formation of a red colour, and by phospho-tungstic acid and hydrochloric acid. They all reduce sulphate of copper in the presence of a caustic alkali, the higher members striking a violet, the lower a pink colour. On heating one of the group with nitric acid and, after cooling, adding ammonia, usually known as the xantho-proteic reaction, a yellow-red colour appears in the solution. Finally, all proteid bodies yield nitrogen on ultimate analysis.

The native proteids, that is, those which occur in living tissues, although they respond to these common tests, are by no means exactly identical one with another.

TABLE XVII.—*The Principal Native Proteids.*

Albumins.—Serum-albumin.
Egg-albumin.
Lact-albumin.
Muscle-albumin.

Globulins.—Fibrinogen (metaglobulin) and fibrin.
Serum-globulin (paraglobulin).
Myosinogen and myosin.
Muscle-globulin.
Vegetable globulins.

n Reagents.

	bumoses.		Peptone.	Mucin.
	etero.	Deutero.		
1. On boiling if some present	—	—	—	—
2. On additi nitric ac	pitated. on heating	—	—	—
3. Trichlorac	Do.	—	—	
4. Picric acid	Do.	—	Precipitated. Soluble on heating	
5. Dilution w Salt ac	P. ld dissolves	— —	— —	P.
6. Saturation sulphate	—	—	—	
7. Half satur nium sul	—	—	—	—
8. Saturation sulphate *a.* In t *b.* Att sli		Some P. P.	— —	P. P.
9. Saturation ride		—	—	P.
10. Acid or alk just on neutralis	if hot, if solu- ain little salt	—	—	—
11. Addition o of dilute cold	—	—	—	C.
12. Saturated s acetic aci	recipitated. on heating		—	
13. Potassio-m HCl	on heating)	P.	P. (Soluble on heating)	C.
14. Acetic acid of potassi		P.	—	—
15. Phospho-w the prese acid		P.	P.	P.
16. Dialysis, a passage t brane	ght. ted in tube	Considerable	Marked	None
17. Biuret	pper present in amount. more	Rose	Rose	Violet
18. Xanthoprot	+	+	+	+
19. Reaction of tion	aline		?	Acid

TABLE XVIII.—*The Reactions of Proteid Bodies to various Common Reagents.*

	Albumin.	Globulin.	Nucleo-Albumin.	Acid Albumin.	Alkali Albumin.	Albumoses.			Peptone.	Mucin.
						Proto.	Hetero.	Deutero.		
1. On boiling when slightly acid if some neutral salts are present	C.	C.	—	—	C.	—	—	—	—	—
2. On addition of cold, strong nitric acid	C.	C.		C.	C.	P.	Precipitated. Soluble on heating	—	—	—
3. Trichloracetic acid - - -	C.	C.		—	C.		Do.	—	—	
4. Picric acid - - - -	C.	C.		C.	C.		Do.	—	Precipitated. Soluble on heating	
5. Dilution with distilled water -	—	P.		—	—	—	P.	—	—	P.
Salt added afterwards -	—	Dissolves slowly, if P. recent		—	—	—	Hot or cold dissolves	—	—	
6. Saturation with magnesium sulphate	—	P.		—	—	—	—	—	—	
7. Half saturation with ammonium sulphate in the cold	—	P.		—	—	—	—	—	—	—
8. Saturation with ammonium sulphate—										
a. In the cold - - -	P.	P.		P.	P.	P.	P.	Some P.	—	P.
b. At the boiling point and slightly acid	C.	C.		P.	C.	P.	P.	P.	—	P.
9. Saturation with sodium chloride	P.	P.		P.	P.	P.	P.	—	—	P.
10. Acid or alkali added to point just on the acid side of neutralisation	—	—		P.	P.	—	P. Especially if hot, if solution contain little salt	—	—	—
11. Addition of a small quantity of dilute organic acid in the cold	—	P.	P.	—	P. or — Depending on amount of alkali present	—	—	—	—	C.
12. Saturated sodium chloride and acetic acid	P.	P.		P.	P.		Partly precipitated. Soluble on heating		—	
13. Potassio-mercuric iodide, and HCl	C.	C.		C.	C.	P.	P. (Soluble on heating)	P.	P. (Soluble on heating)	C.
14. Acetic acid and ferrocyanide of potassium	C.	C.		C.	C.	P.	P.	P.	—	—
15. Phospho-wolframic acid in the presence of a mineral acid	C.	C.		C.	Not if the solution be strongly alkaline	P.	P.	P.	P.	P.
16. Dialysis, amount capable of passage through the membrane	None or trace	None, proteid precipitated in tube		None or trace	None or trace	Slight	Slight. Precipitated in tube	Considerable	Marked	None
17. Biuret - - - - - -	Violet	Violet		Violet if alkali sufficient	Violet	Rose	Rose if copper present be small in amount. Violet if more	Rose	Rose	Violet
18. Xanthoproteic - - -	+	+		+	+	+	+	+	+	+
19. Reaction of pure proteid solution	Alkaline	?		Alkaline	Acid	Alkaline	Alkaline		?	Acid

C = Coagulation. P = Precipitation.

Artificially altered Native Proteids.

Albuminates.—Acid-albumin.
Alkali-albumin.
Ash-free-albumin and globulin.
Coagulated and precipitated albumins and globulins.

Proteids combined naturally with other Substances.

Nuclein (albumin combined with phosphoric acid or a nucleic acid).
Nucleo-albumin (nucleo-proteid), a proteid combined with nuclein, as casein.
Glycoproteid (proteids combined with a carbo-hydrate), mucin, mucoids, hyalogens.
Hæmoglobins (combined with iron), hæmoglobin, oxy-, meta-, and reduced hæmoglobin.

In addition to these proteids there is a large class of substances which may be called albuminoids, and which correspond very closely in composition and reaction to the true members of the proteid group. In this class keratin, elastin, and gelatin may be placed, the first rich in sulphur, the second free from that element, and the third containing a small quantity. Of the three, gelatin is the most unlike a true proteid. It would be out of place in this volume to give an account of the numerous differential tests to which the various members of the proteid group respond. A short statement of their principal characteristics must suffice. (Table XVIII.)

Albumins are soluble in distilled water, and are not precipitated by saturation of their solutions with magnesium sulphate; while, on the contrary, globulins require a certain proportion of a neutral salt in water before they can dissolve, and they are precipitated in a saturated solution of magnesium sulphate, or in a half-saturated solution of ammonium sulphate. Similarly, acid and alkali albumins are not soluble in neutral solutions, but require a certain amount of acid or alkali respectively to keep them in a soluble form. Ash-free albumins are insoluble in water (Bülow, *Pflüger's Arch. f. d. ges. Phys.*, lviii. s. 207), easily dissolved in solutions of acids and alkalies, the acid solutions being very readily precipitated by the addition of neutral salts, the alkaline solutions indifferent to these. Solutions of albumins in distilled water, containing a minimum of mineral matter, are not coagulated by heat even on the addition of acetic acid, but the addition of a very small quantity of a neutral salt to the mixture at once causes the proteid to fall in a coagulated form. The

different proteids do not all coagulate at the same temperature, and this difference has been made use of, especially by Halliburton, to identify and separate individual proteids from a solution containing several members of the group.

For example, if the plasma which can be obtained from the juice of raw muscle be heated gradually, at 47° C. paramyosinogen, at 56° myosinogen, and at 63° myo-globulin are precipitated (these are all globulins); if the solution be further heated, at 73° C. myo-albumin coagulates out. The method of fractional heat-coagulation of proteids is, however, rendered of less service as a means of identification of these bodies than was at one time anticipated, owing to the variations in the coagulation point when different amounts of salts are present.

All native proteids are capable of being split up into less complex and more highly hydrated derivatives. This may be achieved by simply heating their solutions in distilled water at a high temperature and under pressure, or by the action of dilute acids at medium temperatures for a prolonged period, or of stronger acid solutions for a shorter time. When heated with baryta water, or after very prolonged treatment as just described, the process of decomposition goes further, and ends in the formation of various amido-acids, belonging both to the fatty and the aromatic series. These changes are effected in animal and vegetable forms at the temperature of the air, or of the body, by dilute acids and alkalies aided by special ferments. The further reduction to amido-acids is not effected by digestion with acids, but pertains only to that form of digestion in which an alkali is the active agent. The action of a dilute acid or alkali in excess, unaided by a ferment, can go no further at the ordinary or body temperature than the formation of an acid or alkali proteid. These bodies, often termed albuminates, appear to be compounds of the particular acid or alkali in action and the original proteid molecule. The alkali-albumin, however, contains less nitrogen, and the part of the sulphur which is easily split off from native and acid albumins appears also to be absent from its molecule (Neumeister), though this may be due to the action of the combined alkali. A further account of the properties and significance of these bodies will be found in the description of peptic digestion.

So far, then, and no further, can unaided dilute acids and alkalies act on proteids at ordinary temperatures. With the assistance of ferments the process goes much further. All proteids are decomposed by peptic or acid digestion, save only mucin, keratin, and nuclein, and these are simplified by alkaline digestion. The first step in all digestive processes is the formation of acid or alkali albumin, and these bodies, as digestion goes on, are split up into albumoses, and these in turn into peptone. Kühne, in his classic work on the products of proteid digestion, enunciated the theory that all proteid bodies when split up by the action of hydrolytic agents form two groups of derivatives, a *hemi-* and an *anti-*group. By the continued action of the active agent the members of both groups are ultimately transformed through progressive stages

into molecules of *hemi-* and *anti*-peptone respectively. The peptone of the *hemi*-group is less stable than that belonging to the other, and can be further decomposed by tryptic digestion into chemical bodies of comparatively simple constitution, such as leucin, tyrosin, and glutamic acid. The *anti-peptone* cannot be further split up. The antecedent albumoses to each of these peptones are termed *hemi-albumose* and *anti-albumose.*

FATS.

Fats are either of animal or vegetable origin, and are found within the cells of the organism or suspended in the circulating fluids. A fat or hydro-carbon contains carbon, hydrogen, and oxygen in a proportion different to that found in a carbo-hydrate. The natural fats are compounds of a monatomic fatty acid, such as stearic, oleic, or palmitic acids, and a triatomic radical propenyl or glyceryl. Three molecules of the acid combine with one of the radical. The fats derived from these acids are termed stearin, olein, and palmitin. Similarly, butyrin is derived from butyric acid.

$$\text{Tripalmitin}\ \left.\begin{matrix} C_{16}H_{31}O_2 \\ C_{16}H_{31}O_2 \\ C_{16}H_{31}O_2 \end{matrix}\right\} C_3H_5 + \overset{\text{Water.}}{3H_2O} = \overset{\text{Glycerine.}}{C_3H_5(OH)_3} + \overset{\text{Palmitic Acid.}}{3\,(C_{16}H_{32}O_2)}$$

Tristearin ...$C_3H_5\ (C_{18}H_{35}O_2)_3$
Triolein .....$C_3H_5\ (C_{18}H_{33}O_2)_3$
Tributyrin ..$C_3H_5\ (C_4H_7O_2)_3$

Beeswax is an animal fat formed from a cetyl alcohol radical, from which spermaceti is also derived. Waxes can be saponified, but are incapable of digestion. Saponification of fats on boiling them with an alkali results from the combination of the alkali with the fatty acid, the glycerine being set free. Fats are insoluble in water, but may be suspended in the form of very minute droplets as an emulsion if such bodies as gum or albumin be added. When some free fatty acid is present a permanent emulsion may be formed by the addition of sodium carbonate, a reaction which normally occurs in the small intestine. Fats vary much in consistence. Vegetable fats are usually fluid, with only one or two exceptions. Animal fats are fluid at the temperature of the body, but solidify on cooling. Depositions of fat vary in composition in different parts of the body, and vary in their properties in relation to the proportion of olein, stearin, and palmitin present.

TABLE XIX.—*Table of Fats.*

Fat.	Character.	Melting Point.	Solubility.				Where found.	Crystals.
			Alcohol.		Ether.			
			Cold.	Hot.	Cold.	Hot.		
Tristearin	Solid	66.5° Cent.	Insoluble.	Soluble	Slightly soluble	Soluble	In animals only	Brilliant quadrangular plates
Tripalmitin	Solid	45-60° Cent.	Partly soluble	Soluble	Partly soluble	Soluble	In animals and veg'tables	Fine needles
Triolein	Liquid Dissolves other fats at 30°	10° Cent.	Slightly soluble.		Soluble		Chiefly in vegetables	Solidifies at 10° C.
Butyrin	Liquid	....	....		....		Butter	....
Spermaceti	Solid	50° Cent.	....		....		Brain of sperm whale	Crystalline

TABLE XX.—*Composition of the Adipose Tissues of Man and the Domestic Animals.*

Source.	Composition per cent. Water.	Membranes.	Fat.	Chemical Composition of Fat per cent. C.	H.	O.	Melting Point.	Colour.	Chief Fat Present.
Man—From the skin - - Do. abdomen -	29.92	2.5	67.58	76.80 76.44	11.94 11.94	11.26 11.62	36°-41° C.	Yellow	Olein
	15 (Volkmann)	2.5	82.5	....	....	....	....	....	....
Horse - - - - - -	....	....	....	77.07	11.69	11.24	30° C.	Yellow	Olein
Ox - - - - - -	9.96	1.16	88.88	76.50	11.90	11.59	43° C.	White	Stearin and Palmitin
Sheep - - - - - -	10.48	1.64	87.88	76.61	12.03	11.36	46° C.	White	Stearin
Pig - - - - - -	6.44	1.35	92.21	76.54	11.94	11.52	30°-41° C.	White	Olein
Dog - - - - - -	....	....	....	76.63	12.05	11.62	....	....	....
Cat - - - - - -	....	....	....	76.56	11.90	11.43	....	....	....
Mean - - -				76.64	11.92	11.44			

In the formation of adipose tissue, *i.e.*, the laying on of fat, the protoplasmic contents of the cells are gradually replaced by globules of oil, the nucleus being pushed to one side. In vegetable cells fat may arise directly through protoplasmic activity from carbonic dioxide and water, but it also may be formed from starch.

An interesting fact has been noted by Noël Paton in connection with the fat of the porpoise. The layer of fat immediately under the skin of that animal remains fluid at a lower temperature than the fat deposited round the internal organs. The significance of this will at once be seen when it is remembered that the external fat is more exposed to the low temperature of the surrounding water.

Table XIX. gives a list of the chief individual fats, and Table XX. the composition of the compound fats found in the animal body.

Lecithin is a phosphorised fat found in almost all growing cells and in the white corpuscles of the blood. Unlike ordinary fats, it contains nitrogen and phosphorus, but when boiled with baryta water yields barium stearate, neurin, and glycero-phosphoric acid.

Margarin is not a special fat but a mixture of stearin and palmitin, often occurring in the form of fine crystals in fat cells.

CHAPTER VII.

Digestive Processes in the Body.

Action of Saliva on Starch—Dextrins—Maltose—Effect of Acids—Digestion in the Stomach—Production of Hydrochloric Acid—Maly's Views—Kœppe—Gamgee—Acidity of the Stomach Contents—Determination—Variations—Peptic Digestion of Proteids—Relative Digestive Power of Acids—Combination of Acids with Proteids—Cause of Simplification of Proteid Bodies.

The Action of the Saliva on Starch.—The action of the diastatic ferment of the saliva on starch has been so thoroughly investigated that this appears to be the proper place to take up in detail the changes which starch undergoes during its conversion into true sugars. In 1831 Leuchs ascertained that when starch was mixed with saliva it gradually dissolved with the production of a body possessing most of the properties of grape-sugar. Some years later, Mialhe, by the addition of alcohol, precipitated an organic body from saliva, which possessed the same power as the original fluid. This body, he found, was able to convert two thousand times its weight of starch into sugar. Before this it had been known that when starch is boiled with dilute sulphuric acid a sugar is formed. Then it was found that the first stage in the conversion of starch into sugar, either by means of dilute acids and heat, or by the action of diastase, is the formation of an isomer of starch, dextrin; so called because of its optical properties. Up to the time of Dubrunfaut, in 1847, and of the researches of O'Sullivan, the sugar formed from dextrin in the second stage of the process was regarded as dextrose. These observers showed it to be a sugar of the cane-sugar or disaccharide class, and gave it the name of maltose. Soon after this, the identity of the sugar formed by the action of diastase, with that produced under the influence of ptyalin in the saliva, and amylopsin in the pancreatic juice, was established. Musculus and von Mering in 1878 (*Zeitschrift f. phys. Chemie*, vol. i.) showed

that the action of dilute sulphuric acid was not, as had been thought, of the same nature as that of the diastatic ferments. Musculus supposed that the phenomena caused by the action of these ferments are not those simply of hydration, but of decomposition, in which the starch molecule, a molecule of very complex structure, split up into dextrin and maltose, further action splitting up the dextrin into a less complex dextrin and sugar, and, during the continued action of the ferment, this process was repeated until the starch had been converted for the most part into sugar, leaving a small amount of dextrin unacted on. Brown and Heron confirmed this view in 1879, and enlarged it; while the first-named, along with Morris, has thrown much additional light on the process of conversion of the complex starch molecule into simpler molecules of sugar. The best method of testing the action of the saliva, or any other liquid containing a diastatic ferment, consists in the use of a standard starch mucilage containing one gramme of pure potato-starch in 100 c. cm. of distilled water (Roberts). The starch should first be washed with water, treated with a very weak solution of potassium hydrate, then with a one per cent. solution of hydrochloric acid. It should then be washed until all trace of the acid has disappeared, and dried at from 25 to 30° C. It is then mixed with a little cold water in a mortar, and thrown into boiling water with frequent stirring. The mixture should be kept boiling for two or three minutes (Brown and Heron). Liquefaction occurs almost immediately on the addition of a diastatic ferment to some of this starch-paste kept at a temperature of about 30-50° C. If the ferment be small in amount the change occurs more slowly, and if the ferment be added in less and less proportion, a point is reached at which this formation of soluble starch is the only change taking place, no dextrin or sugar being formed. This soluble starch may be regarded as the first step in the simplifying of the large and composite insoluble starch molecule, without any change in its elementary composition. Soluble starch is coloured blue by iodine, and is precipitated from its solutions by alcohol and by tannic acid, like insoluble starch, but unlike dextrins and maltose. If iodine be added to the mixture after the action has gone on for a short time, a red colour appears; if there is still some soluble starch present, the presence of the red alters the blue colour previously produced by iodine to a purple, more and

more reddish in tint in proportion to the amount of erythrodextrin present. The soluble starch can be removed by precipitation with tannic acid, the erythrodextrin remains. If alcohol be added, it, in like manner, may be got rid of, leaving a sugar, maltose, in the filtrate. Two erythrodextrins have been described, but their existence as actual substances is regarded by some as doubtful, the reactions presented by them being ascribed to varying mixtures of lower dextrins and unconverted starch. Further action of the ferment produces other dextrins from erythrodextrin, probably progressively, the one from the other, with at the same time the formation of maltose. The addition of iodine to solutions of these lower dextrins, achroodextrin and maltodextrin, is not followed by any colouration, and forms Roberts' *achromic point*. The time taken by a certain amount of a diastatic fluid to render a constant quantity of starch-paste achromic is used as an indication of the power of its ferment. If a large quantity of ferment be added to a sufficiently dilute starch-paste, the achromic point may be reached practically instantaneously. Roberts has shown that the amount of starch converted varies directly with the quantity of the ferment employed, while the time taken to reach the achromic point is practically in inverse ratio to the quantity of ferment.

TABLE XXI.—*The amount of Solids found in Saliva per mille.*

	Total Solids.	Organic Matter.	Ash.
I. *Parotid Saliva*—			
Man	13.485	6.220	7.265
Sheep	11.000	1.000	10.000
Cow	9.300	0.440	8.860
Horse	8.540	4.300	4.240
Dog	7.184	1.743	5.441
II. *Submaxillary Saliva*—			
Dog	11.700	6.432	5.268
Cow	8.860	3.530	5.330
Horse	7.500	4.925	2.575
Man	4.100	2.900	1.200
III. *Sublingual Saliva*—			
Dog	15.750	3.450	12.300
IV. *Mixed Saliva*—			
Sheep	11.000	1.000	10.000
Dog	10.400	3.610	6 790
Cow	9.300	0.440	8.860
Horse	8.000	2.000	6 000
Man	5.880	3.860	1.920

TABLE XXII.—*Composition of Saliva, per* 1000 *parts, in Man, Dog, Horse, Sheep, and Cow.*

	Water.	Solids.	Organic Matter.	Sulphocyanide of Potash.	Chlorides.	Carbonate of Lime.	Total Ash.
I. *Parotid*—							
Man (Mitscherlich)	983.7-985.4	14.6-16.3	9.0	0.3	5.0		5.6-7.3
,, (Hoppe-Seyler)	993.16	6.84	3.44	—	3.4		3.4
,, (Van Setten)	983.8	16.2	—	—	—		—
Dog (Schmidt)	995.3	4.7	1.4	—	2.1	1.2	3.3
,, (Hector)	993.5-991.5	6.1-8.47	1.53	—	6.251	0.688	4.57-6.91
,, (Werther, Mean of 3)	992.2	7.8	2.3	—	1.34	—	5.5
Horse (Lehmann)	990.0	10.0	2.06-6.0	—	4.8-8.73		7.94-4.00
,, (Smith)	992.92	7.08	4.84 (*circa*)	—		1.24	2.14
Cow (Lassaigne)	990.7	9.3	0.44	—	2.85	3.38	8.86
Sheep (Smith)	989.0	11.0	1.00	—	6.0	3.0	10.0
II. *Submaxillary*—							
Man	996.4-995.4	3.6-4.6	2.4-3.4	0.04	—	—	1.2
Dog (Werther)	987.7	12.3	—	—	3.35	—	—
,,	988.7	11.3	6.6	—	1.50	—	4.7
,,	983.2	16.8	10.2	—	3.29	—	6.6
,,	987.4	12.6	6.2	—	—	—	6.4
,, (Smith)	994.4	5.6	2.11	—	—	—	3.85
Horse ,,	992.5	7.5	4.925	—	—	—	2.5-7.5
Cow ,,	991.14	8.86	3.53	—	—	—	5.33
III. *Sublingual*—							
Dog (Werther)	978.8	21.2	—	—	7.06	—	—
,,	984.7	15.3	1.9	—	10.80	—	13.4
,,	986.3	13.7	4.3	—	8.14	—	9.4
,,	987.2	12.8	3.4	—	—	—	9.4
IV. *Mixed*—							
Man (Mean of 6)	994.12	5.88	3.86	0.08	1.188	—	1.92
Horse	992.00	8.00	2.00	—	4.92	—	6.00
Cow	990.70	9.30	0.44	—	2.85	—	8.86
Dog	989.60	10.40	3.61	—	5.82	—	6.79
Sheep	989.00	11.00	1.00	—	6.00	—	10.00

If one molecule of soluble starch be looked upon, with Roberts, as $10(C_{12}H_{20}O_{10})$, $8(H_2O)$ or ten simple starch molecules with eight molecules of water, the actual changes occurring may be thus represented:—

Soluble starch equals—

TABLE XXIII.

1.	Erythrodextrin	*a.*	$9(C_{12}H_{20}O_{10})$	$(C_{12}H_{22}O_{11})$	(Maltose).
2.	Do.	*b.*	$8(C_{12}H_{20}O_{10})$	$2(C_{12}H_{22}O_{11})$	do.
3.	Achroodextrin	*a.*	$7(C_{12}H_{20}O_{10})$	$3(C_{12}H_{22}O_{11})$	do.
4.	Do.	*b.*	$6(C_{12}H_{20}O_{10})$	$4(C_{12}H_{22}O_{11})$	do.
5.	Do.	*c.*	$5(C_{12}H_{20}O_{10})$	$5(C_{12}H_{22}O_{11})$	do.
6.	Do.	*d.*	$4(C_{12}H_{20}O_{10})$	$6(C_{12}H_{22}O_{11})$	do.
7.	Do.	*e.*	$3(C_{12}H_{20}O_{10})$	$7(C_{12}H_{22}O_{11})$	do.
8.	Do.	*f.*	$2(C_{12}H_{20}O_{10})$	$8(C_{12}H_{22}O_{11})$	do.

The total equation may be represented as—

$$\underset{\text{Soluble Starch.}}{10(C_{12}H_{20}O_{10})}\ \underset{\text{Water.}}{8H_2O} = \underset{\text{Maltose.}}{8(C_{12}H_{22}O_{11})}\ \underset{\text{Achroodextrin.}}{2(C_{12}H_{20}O_{10})}.$$

Represented in this way, each successive step consists in the removal of one of the primary starch molecules, which, added to the elements of water, becomes maltose. The accompanying table, after Sir William Roberts, explains the process in detail (Table XXIV.). The achroodextrin left unconverted into maltose at the end of the reaction is only with difficulty acted on by ferments, but is converted into sugar by the action of dilute sulphuric acid and heat. No notice is taken in the above scheme of malto-dextrin, a body found during the action of diastatic ferments under certain conditions. Unlike achroodextrin it possesses a slight reducing power, and is regarded by Brown and Morris as being composed of one molecule of maltose and two primary dextrin molecules, thus—

$$\underset{\text{Malto-dextrin.}}{\begin{pmatrix} C_{12}H_{22}O_{11} \\ (C_{12}H_{20}O_{10})2 \end{pmatrix}} + \underset{\text{Water.}}{2H_2O} = \underset{\text{Maltose.}}{3C_{12}H_{22}O_{11}}.$$

TABLE XXIV.—THE CARBO-HYDRATE GROUP.—*From Starch to Glucose and Alcohol.*

		Molecular Weight.
1 Molecule of insoluble starch	$= [(C_{12}H_{20}O_{10})_{10}]_5$	16200
is equal to 5 Molecules of soluble starch	$= [(C_{12}H_{20}O_{10})_{10} + 8\ H_2O]_5$	16920
while 1 Molecule of soluble starch	$= (C_{12}H_{20}O_{10})_{10} + 8\ H_2O$	3384

One molecule of soluble starch can yield during the progressive action of hydrating bodies:—

		Dextrins.	Water.	Maltose.		Molecular Weights. Dextrin.	Water.	Maltose.	Total.
1.	Erythrodextrin	α 9 $(C_{12}H_{20}O_{10})$	+ 7 H_2O +	$(C_{12}H_{22}O_{11})$	...	324 × 9	+ 18 × 7	+ 342	= 3384
2.	Do.	β 8 $(C_{12}H_{20}O_{10})$	+ 6 H_2O +	2 $(C_{12}H_{22}O_{11})$	...	324 × 8	+ 18 × 6	+ 342 × 2	= 3384
3.	Achroodextrin	α 7 $(C_{12}H_{20}O_{10})$	+ 5 H_2O +	3 $(C_{12}H_{22}O_{11})$	...	324 × 7	+ 18 × 5	+ 342 × 3	= 3384
4.	Do.	β 6 $(C_{12}H_{20}O_{10})$	+ 4 H_2O +	4 $(C_{12}H_{22}O_{11})$	...	324 × 6	+ 18 × 4	+ 342 × 4	= 3384
5.	Do.	γ 5 $(C_{12}H_{20}O_{10})$	+ 3 H_2O +	5 $(C_{12}H_{22}O_{11})$	...	324 × 5	+ 18 × 3	+ 342 × 5	= 3384
6.	Do.	δ 4 $(C_{12}H_{20}O_{10})$	+ 2 H_2O +	6 $(C_{12}H_{22}O_{11})$	...	324 × 4	+ 18 × 2	+ 342 × 6	= 3384
7.	Do.	ϵ 3 $(C_{12}H_{20}O_{10})$	+ 1 H_2O +	7 $(C_{12}H_{22}O_{11})$	...	324 × 3	+ 18	+ 342 × 7	= 3384
8.	Do.	θ 2 $(C_{12}H_{20}O_{10})$	+ 0 +	8 $(C_{12}H_{22}O_{11})$	...	324 × 2	+ 0	+ 342 × 8	= 3384
9.	Do.	μ 1 $(C_{12}H_{20}O_{10})$	+ 1 H_2O* +	9 $(C_{12}H_{22}O_{11})$	...	324		+ 342 × 9	= 3402
10.	—		+ 2 H_2O +	10 $(C_{12}H_{22}O_{11})$	...			+ 342 × 10	= 3420

* In 9 and 10 the water molecules are additional to those supposed to be present in a molecule of soluble starch.

Maltose.		Water.		Glucose.	Corresponding Molecular Weight.		Total.
10 $(C_{12}H_{22}O_{11})$	+	10 (H_2O)	=	20 $(C_6H_{12}O_6)$	(180 × 20)	=	3600

= 1 molecule of soluble starch
+ 12 molecules of water.

Glucose.		Ethylic Alcohol.		Carbonic Acid.	
20 $(C_6H_{12}O_6)$	=	40 (C_2H_6O)	+	40 (CO_2)	(46 × 40) + (44 × 40) = 3600

If a compound molecule of insoluble starch be (with Roberts) supposed to consist of five molecules of soluble starch, on the addition of 8 H_2O to each, the compound molecule will represent on the addition of—

	1.	40	molecules of water	= 5	molecules of soluble starch.		
or	2.	40	do.	do. 5	do.	erythrodextrin α	+ 5 maltose.
	3.	40	do.	do. 5	do.	do. β	+ 10 do.
	4.	40	do.	do. 5	do.	achroodextrin α	+ 15 do.
	5.	40	do.	do. 5	do.	do. θ	+ 40 do.
	6.	50	do.	do. 50	molecules of maltose.		
	7.	100	do.	do. 100	do.	glucose.	
	8.	100	do.	do. 200	do.	alcohol + 200 molecules CO_2.	

The end product of the digestion of starch consists of the sugar known as maltose. It is isomeric with cane-sugar, but loses one molecule of water when its crystals are dried at 100° C. It is dextro-rotatory, rotating the plane of polarised light to the right, and reduces Fehling's copper solution, but to a much less extent than glucose. If the reducing power of glucose be regarded as equal to 100, that of the same amount of maltose is only equal to 65. It is easily fermented by yeast. It is said that in a mixture of maltose and dextrose the maltose disappears under the action of yeast before the dextrose is affected. Boiled with dilute sulphuric acid it yields 98 per cent. of its weight of dextrose.

The diastatic ferment of the saliva produces this change in starch more energetically as the temperature rises from 0° to 30° C.; it is most active between that point and 45° C., and becomes less powerful above this, until from 65° to 70° C. all conversion ceases. (See Chart I.)

Although the products of vegetable diastase and the animal amylolytic ferments are the same, the ferments exhibit several points of difference. Thus malt-diastase is most active at 60° C., and only ceases to act at 80° C., while the presence of .05 per cent. of salicylic acid arrests its action, although it requires the proportion of .1 per cent. of this acid to cause the least retardation of the action of the salivary ferment.

The form in which the starch is used has some influence on the ease with which it is converted by ptyalin. Hammarsten found that while maltose could be detected in a few minutes when saliva was added to rye- or maize-starch, a period of two or three hours elapsed before its appearance when raw potato-starch was used. It must also be borne in mind that the granules of raw starch are surrounded by an envelope of cellulose on which the salivary juice has no action. If in the process of boiling these capsules are ruptured, or if in mastication the same thing occurs, the saliva is able to act. Whole granules of raw starch, when swallowed intact, are almost indigestible in man; in the *Herbivora*, however, they are acted on in the rumen and stomach. Glycogen, or animal-starch, an isomer of starch, is acted on by the diastatic ferments in exactly the same way as starch itself. As in the case of other unformed ferments, the action of diastase and ptyalin is retarded, and at length arrested, if the sugar formed be allowed to accumulate in the solution.

Rapidity of Action of Ptyalin.—Roberts gives 4 minutes as the normal period of time which elapses before the achromic point is reached, when 1 c. cm. of human saliva is added to 10 c. cm. of a standard starch mucilage (1 per cent.) at blood-heat. The following table from Roberts shows the rapidity of action in the case of the pancreatic juice :—

TABLE XXV.

10 c. cm. standard starch mucilage, with 90 c. cm. water, and 0.1 c. cm. pancreatic extract, at 40° C.

Time.	Reaction with Iodine.
10.30	Commencement.
10.31	Blue.
10.32	Violet.
10.33	Brown.
10.34	Yellowish-brown.
10.35	Pale yellow.
10.36	No reaction, achromic point.
6 minutes.	

The action of all diastatic ferments proceeds best in a neutral or slightly alkaline medium. It is still active in a faintly acid solution, but is incapable of converting starch in a solution containing 0.1 per cent. of free hydrochloric acid.

The authorities on this subject are, however, by no means at one with regard to the strength of acid required to inhibit or retard the action of ptyalin. Thus Chittenden and Ely (*Journ. of Physiology*, vol. iii.) state that 0.05 per cent. of hydrochloric acid rather increases the action of the ferment, a statement which Astachewsky (*Centralblatt f. med. Wissenschaft*, 1878) upholds. Langley, on the other hand (*Journ. of Physiology*, vol. iii. p. 246), says that ptyalin is destroyed by hydrochloric acid above 0.005 per cent., and is distinctly inhibited by 0.0014 per cent. According to this observer, carbonate of sodium above 0.5 per cent. stops the action of ptyalin. Again, Chittenden and Griswold (*Amer. Chem. Journ.*, vol. iii.) state that a very small quantity of acid added to saliva increases its power, a statement explained by Langley, who found that neutralised saliva is more active than if not neutralised.

But another factor has to be considered. Saliva contains a small quantity of proteid bodies, and free acids combine to a certain extent with proteids. The first portion of the free acid added neutralises the alkali present, the second combines with the proteid, and it is only after the affinities of the proteids present have been satisfied that free acid appears in the solution. Langley thought that the combined acid acted prejudicially on the ferment, but Chittenden and Smith showed that up to a certain point it rather stimulated it. The author found (*Journ. of Anat. and Phys.*, vol. xxvii. p. 201) that while .018 per cent. of hydrochloric acid, mostly in the free state, entirely stopped the action of ptyalin, .0318 per cent. of that acid, when combined with proteids, allowed some conversion to take place, while

.015 per cent. of combined acid had only a slight retarding effect. This point is of value when the question of the digestion of starch in the first stages of gastric digestion is considered, as during the early part of digestion in the stomach the hydrochloric acid secreted by its glands is entirely combined with proteids or inorganic bases. Aitchison Robertson (*Edin. Med. Journ.*, May 1896) used filtered gastric contents in an investigation into this subject, and found that small quantities of acid contents hindered or inhibited the action of ptyalin. As he made no observations on the state of the acid contained in the specimens employed, and neglected to take into account the alkalinity of the saliva added, his conclusions in many particulars require revision. After the introduction of starch mucilage into the stomach by the stomach tube, however, he found that some conversion took place under normal conditions, but that it was very slight in amount, whereas in disease, with a lessened acidity, most of the starch introduced was transformed into dextrins and maltose.

The Gastric Juice.—The composition of the gastric juice of man, and of the dog and sheep, is depicted in Table XXVI. The greater part of the organic solids given in it may be taken to represent the ferment pepsin. The proportion of hydrochloric acid present varies in different animals, the gastric juice of the dog containing about .3 to .4 per cent.; of man, .2 to .3 per cent.; and of the sheep, only from .1 to .15 per cent.

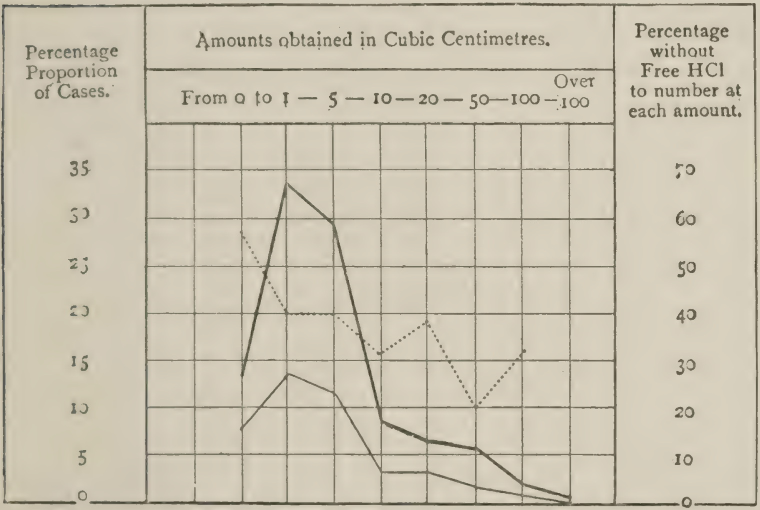
The amount of gastric juice secreted varies so much under different conditions that little value can be placed on the estimates of observers. Schmidt reckoned the flow at 500 grammes per hour in man. The total gastric secretion per diem of the dog has been stated to be $\frac{1}{10}$ of the body-weight, and if the same proportion obtains in man the total daily secretion will equal 6 to 6.5 kilogrammes.

TABLE XXVI.—*Composition of Gastric Juice (per mille).*

	Man.	Dog.	Sheep.
Water	994.40	973.062	986.14
Total solids	5.60	26.938	13.86
Organic solids (Burnt off)	3.39	20.645	5.78
Ash	2.21	6.293	8.08
Carbonate of potassium	0.55	1.125	1.52
Chloride of calcium	0.06	0.624	0.11
,, sodium	1.46	2.507	4.37
,, ammonium	—	0.468	0.47
Phosphate of calcium	0.125 (calcium, magnesium, iron)	1.729	1.18
,, magnesium		0.226	0.57
,, iron		0.082	0.33
Hydrochloric acid	0.2 (?) (2.0)	3 050	1.26
Chlorine	1.368 (3.078)	5.720	4.97
Volatile	0.19 ? (1.9)	3.270	1 53
Inorganic	1 178 (1.178)	2.450	3 44

Gintl, working under Riegel (*Münchener Med. Wochenschrift*, 1897, No. 23), found, as the result of measuring 189 specimens of fluid obtained through the stomach tube from the human stomach in health after fourteen hours abstinence from food, that the quantity was usually small, averaging about 9 c. cm. ; while in 40 per cent. no free hydrochloric acid could be identified. Chart III. shows the chief points of Gintl's investigations. It is apparent from it that the most frequent quantity obtained varied from 0 to 1 c. cm., while in only one case was it above 100 c. cm. Further, it is evident that those specimens with the smaller amounts of fluid more commonly contain no free hydrochloric acid.

CHART III.—Showing the quantity of Stomach Contents removed $14\frac{1}{2}$ hours after Food, with the frequency of the presence of Free HCl. Number of observations, 189.



Percentage number yielding the various quantities of Fluid ————

Percentage number which did not show the presence of Free HCl ————

Percentage of cases without Free HCl to total numbers yielding the different amounts of fluid ....

The Production of the Hydrochloric Acid of the Gastric Juice.—Since it was proved that hydrochloric acid formed the principal acid present in the gastric juice, various attempts have been made to explain the chemical method by which it is separated from the blood serum by the gastric glands. It may be first assumed that the acid is derived from the chlorides of the body, especially as it has been shown that the formation of the acid ceases when food is given containing no chlorine compounds. Grützner (*Neue Untersuchungen über die Bildung und Ausscheidung der Pepsin*, Breslau, 1875) has observed that the gastric mucous membrane contains most pepsin when it is richest in chlorides. Bence Jones, Roberts, and Maly have found that the acidity of the urine diminishes or may disappear during active digestion. Among the various theories which have been broached to explain how the hydrochloric acid is formed, Brücke's hypothesis that, under the influence of the secretory nerves of the stomach, the gastric glands possess the power of decomposing chlorides electrolytically, and of directing the resulting acid towards the outer surface of the mucous membrane, the bases towards the blood-stream, may be looked upon as purely speculative and to rest on no firm foundation. Ralfe showed, however, that if a weak current of electricity was passed through a U-tube, one limb of which contained a solution of sodium bicarbonate, the other a solution of sodium chloride, with a dialysing membrane between the two solutions, the liquid at the positive pole became acid, and that at the negative became alkaline. The reaction which occurs in this experiment depends upon the formation of hydrochloric acid and carbonate of sodium from the two salts employed. That such a force is in active operation in the body rests only on theory, and has not been proved in fact.

Maly found that if chloride of an alkaline metal is mixed with lactic acid and the mixture dialysed, free hydrochloric acid diffuses through, the result of the chemical action being the formation of a lactate and hydrochloric acid, in addition to the remainder of the chloride and lactic acid unacted upon. But he found that there is no formation of lactic acid in the body by which such a chemical reaction can be brought about, and concluded that the free hydrochloric acid of the gastric juice arises from some other form of decomposition of chlorides. Maly, again, has published a more recent theory. He regards the formation of the

hydrochloric acid as brought about by interaction between carbonic acid, disodic phosphate, monosodic phosphate, and chloride of sodium both in the blood-stream and in the cells. Hydrochloric acid possesses a remarkably high power of diffusion, and we have only to look upon the glands of the stomach as forming a very delicate diffusion apparatus to account for the separation of the acid set free by the above chemical process. Against this theory we may advance the objection that if hydrochloric acid be already formed in the blood we should expect it to be secreted by the kidney as well as by the stomach. Also, the interactions suggested by Maly are not all located by him in the cells of the gastric glands, and if his proposition be correct free hydrochloric acid will be present in the general blood-stream, as well as in the serum which passes through the cells of the gastric glands.

Kœppe (*Pflüger's Arch.*, lxii. s. 567) has suggested that the osmotic pressure of the blood-plasma has to do with the formation of hydrochloric acid. He estimates the osmotic pressure of blood by Hedon's hæmatokrit against a solution of cane-sugar. He notes that salts give off no warmth themselves, but do work when passing into solutions. He finds that the osmotic pressure of the blood rises on the addition of salts to it, and in this way water may be secreted into the stomach. He says that the acid of the gastric juice is not formed in the gland cells themselves but in their walls, in virtue of their specific properties, which prevent, as a semi-permeable wall, free hydrochloric acid ions passing through, while they allow free hydrogen ions to pass in the other direction. The presence of a secretory stimulus is necessary for the formation of the acid, and this may consist in free chlorine ions on the inner side of the cell wall. He refers also to the formation of hydrobromic and hydriodic acids when chlorine is abstracted from the food, and salts of these acids given in its place.

Gamgee has modified Maly's theory by suggesting that the acid-forming cells of the stomach have peculiar selective powers in reference to certain salts of the blood, as we know the cells of other secreting glands to have. They may be supposed, for instance, to have an affinity for the phosphates of sodium, both alkaline and acid, and for chlorides. If this is granted, we have only to surmise that

the same reactions may occur inside the cells of the gastric glands which take place in similar solutions in the laboratory.

$$2\ Na_2HPO_4 + 3\ CaCl_2 = Ca_3(PO_4)_2 + 4\ NaCl + 2\ HCl.$$

Acid phosphate of sodium.	+	Chloride of calcium (Chloride of lime).	=	Phosphate of calcium.	+	Chloride of sodium.	+	Hydrochloric acid.

The result of this reaction is the production of hydrochloric acid, which, from its great diffusibility, can pass, on being formed in the body of the cells, through the walls into the stomach cavity. This hypothesis removes the seat of the formation of the acid from the general blood-stream to the cells, and is a feasible adaptation of Maly's theory of the chemical processes which probably occur. The theory of Kœppe may be easily brought into line with Gamgee's by supposing that the acid is formed in the walls of the cells and not in the cells themselves.

As the hydrochloric acid of the gastric juice must arise from the chlorides in the blood, and as the reaction suggested by Maly occurs outside the body, the gastric juice should contain the salts corresponding to those found in artificial experiments. If we regard the reaction as an interchange between acid phosphate of soda and chloride of sodium or calcium, we should expect to find phosphates of sodium and calcium, chloride of sodium and free hydrochloric acid in the juice secreted, in like manner to that which we find *in vitro*. And analysis of the gastric juice corroborates this in every particular, for it contains the chloride of sodium and calcium, phosphate of sodium, and phosphates of calcium and magnesium. The magnesium phosphate may be formed, of course, from the chloride in the same manner as that of sodium and calcium. The secretion of free mineral acid by animal cells at first sight appears to be an anomaly. We have seen before, however, that the saliva of a gasteropod, *Dolium galea*, contains free sulphuric acid in very considerable proportion.

The total acidity of the stomach contents may be determined on either filtered or unfiltered specimens. Titration of the unfiltered contents gives the most correct results unless the solid matters have a marked colouration which may interfere with the end reaction. As a rule the acidity of an unfiltered specimen is higher than that of the filtered, owing to the presence of coagulated proteid with its attached acid. On the other hand, if the suspended matter be largely carbo-hydrate in nature, the total acidity

may be lower and give an erroneous impression of the state of digestion. In such cases the determination of the acidity on the filtered contents affords the more reliable results. It is a question whether the greater accuracy obtainable by determining the end of the reaction in the filtered contents does not compensate for the slight difference observed between their acidity and that of the unfiltered contents. To put it in another way, filtration removes the coagulated proteids, with the hydrochloric acid combined with them, and the other insoluble portions of the food, chiefly vegetable in nature; the filtrate containing all the soluble proteids, the acids, free or combined with them, the acid salts, and the soluble carbo-hydrates. The principal object in estimating the total acidity of a sample of stomach contents is to get a figure from which the free acidity can be calculated after determination of the acidity which has combined with proteid bodies. The mere fact of the gastric contents having a certain total acidity is of little consequence unless the component constituents of that acidity are known. In this way it matters little whether the whole analysis is undertaken on an unfiltered or on a filtered specimen, if the fact be noted and the nature of the preceding meal indicated. Undoubtedly the investigation of the unfiltered contents gives a result more akin to the actual state of digestion in the stomach, but, as mentioned above, the colour reactions are of necessity less delicate. If the unfiltered contents are used they must be well shaken beforehand to divide the insoluble particles and to render the fluid uniform. The actual determination of the total acidity is performed by means of a deci-normal, or, if great accuracy is required, a centi-normal solution of sodium hydrate. A normal solution of any chemical substance signifies a solution which contains in each litre as many grammes of the substance as there are figures in its atomic weight. For instance, hydrochloric acid has an atomic weight of 36.5 (H 1, Cl 35.5), and a normal solution of HCl contains 36.5 grammes of the acid in each litre. The exact weight of HCl is 36.46, but for ordinary purposes 36.5 is sufficient. In the same way a normal solution of sodium hydrate is made by putting 40 grammes into a litre measure, and adding distilled water up to the mark. An equal quantity of an acid normal solution exactly neutralises an equal portion of an alkaline normal solution. A deci- or a centi-normal solution is made by diluting the normal solution ten or a hundred times respectively. The indicators used are litmus, cochineal, or phenol-phthalein. Phenol-phthalein is the most delicate, but gives very erroneous results in the presence of ammonia or its salts. Neither litmus nor cochineal can be used with any approach to accuracy if the contents are highly coloured. Phenol-phthalein is colourless in acid solutions, bright red in alkaline. It is unnecessary to point out the advantage gained by the use of an indicator which absolutely changes its colour at the end of titration, over one which merely alters its shade. The strength of the solution of phenol-phthalein is of little consequence, a 2 per cent. solution in alcohol is generally recommended. Litmus may be used in the form of papers, or dissolved in alcohol. Cochineal should also be dissolved in alcohol, care being taken to ensure that the solution is neutral in reaction. The actual process of titration is as follows :—

A measured quantity of the stomach contents is poured into a beaker; the amount is immaterial, but 5 c. cm., 10 c. cm., or 100 c. cm. are the most convenient amounts.

A Mohr's burette is filled with a deci-normal solution of caustic soda, and the point on the scale to which it reaches duly noted. The soda is then added drop by drop to the stomach contents, to which a few drops of the phenol-phthalein solution have been previously added. Whenever the stomach contents exhibit a permanent pink tinge the titration is over. If the contents are tested without filtration the end reaction is often very indeterminate, and it is well to leave the specimen standing for some time after a decided pink tinge has appeared, and to stir it occasionally, as the alkali added takes some time to neutralise the acid bound up in the coagulated proteids.

For example, 10 c. cm. of stomach contents are taken, two drops of phenol-phthalein added, and deci-normal soda dropped in until a permanent pink colour appears in the solution, and 9.5 c. cm. of the soda solution are requisite. As each cubic centimeter of a normal solution of sodium hydrate exactly neutralises 0.0365 grammes of hydrochloric acid, a similar quantity of a deci-normal solution will represent 0.00365 grammes of the acid, 9.5 c. cm. corresponds to (0.00365×9.5) 0.034675 grammes of HCl. But 10 c. cm. were taken, and 0.0346 grammes in 10 c. cm. equals 0.346 in a hundred. The total acidity of the specimen is therefore 0.346 per cent. expressed in terms of hydrochloric acid. To express it in terms of any other acid the atomic weight of the acid required is substituted for that of HCl, care being taken in the case of dibasic acids, such as H_2SO_4, to divide the atomic weight by two before multiplying.

Another method of expressing the acidity has been recommended by Ewald. It has the merit of simplicity, but is hardly so scientific. Ewald suggests that the number of c. cm. of the deci-normal solution of sodium hydrate required to neutralise 100 c. cm. of the gastric contents should be taken as the symbol of its acidity. By this method the acidity of the illustrative sample given above would be 95.

In health, the reaction of the various fluids secreted by the glands concerned in digestion is fairly constant, varying within small limits. Still it is a noteworthy fact that the percentage of acid or alkali in the pure juice, although almost constant under identical conditions in one individual, varies appreciably when samples from different individuals are analysed. How do the cells of the secreting glands know when to cease producing either acid or alkali in the act of digestion? The proportion of free hydrochloric acid, to take gastric digestion as an example, in the pure gastric juice produced by reflex or local mechanical irritation, depends upon the amount of acid secreted by the oxyntic cells and mixed with the secretion of the pepsin-producing glands. The acidity of the mixture thus obtained may be regarded as the normal for the individual. In man it varies from .15 per cent. to .22 per cent.; in the dog, from .23 to .33 per cent.; in the sheep it is about .12 per cent. If the gastric contents of any of these animals be examined shortly after food has been taken, the acidity present will be found to be much

less than that of the gastric juice, provided the food does not contain much acid in itself, while the acid present at this stage is either in the form of an inorganic acid, such as lactic acid, or as hydrochloric acid combined with the proteids of the food. In this condition hydrochloric acid does not give the reactions peculiar to a free mineral acid, although its acid value towards alkalies remains the same. As time goes on the acidity of the contents gradually increases, according to the nature of the food, and if the food consists largely of proteids may even exceed the acidity of the pure gastric juice before the presence of free hydrochloric acid can be detected. If the food be almost wholly composed of carbo-hydrates, free hydrochloric acid appears at an early period and soon reaches its maximum. From some experiments made by the author on artificial peptic digestion in dialysers (*Journ. of Anat. and Phys.*, vol. xxvii.), in which the substance experimented upon was placed inside the dialyser with some pepsin, and a solution of hydrochloric acid of known strength placed outside the parchment, it is clear that the presence of proteid bodies has a great influence on the distribution of hydrochloric acid. When the substance used consisted almost entirely of carbo-hydrates the acidity inside the dialysing tube after a few hours was almost the same as that outside, and was mostly in the free condition. If proteids alone were placed inside the dialyser within the space of from one to two hours the acidity inside was greater than that of the solution outside the tube, although free acid could not be detected in the digesting mixture. Later on, the acidity of the contents of the tube often rose very markedly above that in the surrounding fluid, while the free acid present in it was less. When proteids constituted the bulk of the substance digested in this way the free hydrochloric acid inside the dialyser never equalled the proportion of free acid outside it. That is to say, that however great the percentage acidity of the digesting mixture might be, if it was composed entirely of hydrochloric acid in a state of combination with proteids, free acid could still dialyse through, but not in sufficient amount to equalise the free acidity of both solutions. If a solution of this acid is placed round a dialysing tube filled with water, in time, by the law of osmosis, the acidity outside and within the tube will be equal. If a solution of a pure carbo-hydrate, such as soluble starch, be similarly used, the same thing occurs. Put a proteid body, either in solution or in bulk, into the water in the tube,

the acidity within soon rises above that without. The acid which combines with the proteid must, *ipso facto*, lose all, or nearly all, its dialysing power, and allow more free acid to diffuse through the membrane to preserve the osmotic balance. When the solution in the tube contains proteid bodies and has had pepsin added to it, as digestion proceeds and diffusible products are formed the condition changes. Many of the products of proteid digestion are diffusible and occasion the presence of combined acid outside as well as within the tube, and, in time, the amount of proteid outside may equal that remaining, when the acidities of both approximate. (Chart IV.)

The same phenomenon occurs in the healthy stomach. The greater the proportion of proteid material in the food ingested, the higher does the acidity of the gastric contents rise. In the *Edinburgh Medical Journal* for 1893 the author published some observations bearing on this subject, in which he investigated the effect of carbo-hydrates and proteids on the gastric acidity. The results serve to show that the course of the gastric acidity corresponds to the nature of the food, and to the conditions described above in digestion in dialysers.

An observation by Ellenberger and Hofmeister on the horse corroborates these statements. They found the following acidities to be present in the stomach of that animal:—

TABLE XXVII.

Food.	Hydrochloric Acid.	Organic Acids.
1. Oats and chopped straw	0.163 per cent.	0.287 per cent.
2. Oats	0.490 ,,	0.610 ,,
3. Hay	0.022 ,,	1.798 ,,

The amounts of hydrochloric acid obtained exactly correspond to the proportion of proteid in the food. Oats contains from 12 to 14 per cent. of proteids, hay from 5 to 9 per cent., and straw about 3 per cent. Allowing, then, that the acidity of the gastric contents varies with the character of the food, we are forced to admit the necessity of there being some controlling mechanism through which these changes can be brought about. As in experiments with dialysers, so in the healthy stomach the combined acid appears to have little or no effect on the equilibrium, which must exist between the agents at work in supplying sufficient acid and the amount

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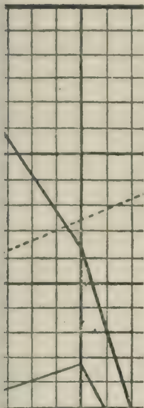


CHART IV.—(i.) Showing the Course of the Total Acidity and the Free Acidity of the Stomach Contents in Man after Proteids and after Carbo-hydrates, with Grützner's data for the relative quantity of Pepsin in the Secretion added.

A. Gastric acidity.
1. After meat.
2. After carbo-hydrates.

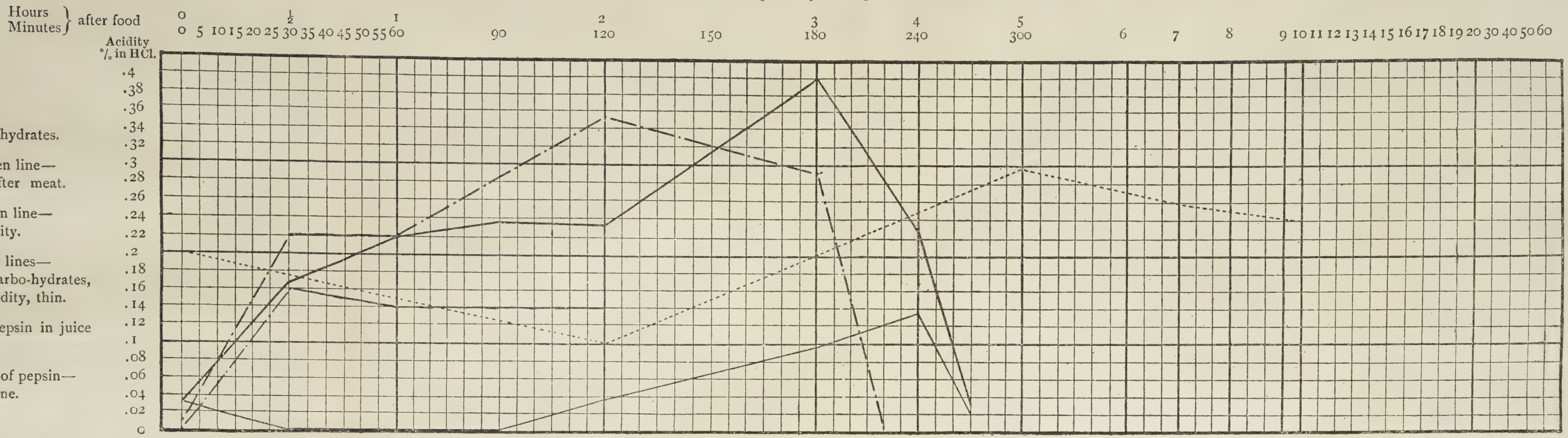
Thick unbroken line—
Total acidity after meat.

Thin unbroken line—
Free acidity.

Dot and dash lines—
Total acidity after carbo-hydrates, thick. Free acidity, thin.

B. Proportion of pepsin in juice (Grützner).

Relative amount of pepsin—
Dotted line.



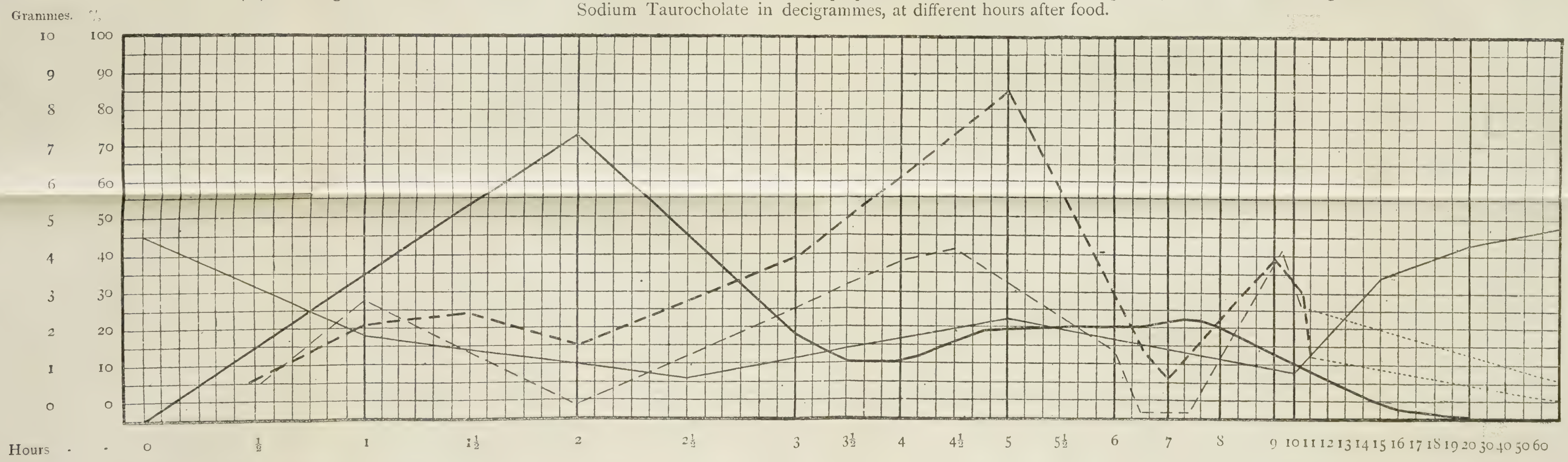
(ii.) Showing the Variations in the amounts of Pancreatic Juice in relative proportion, of its Solids and of the quantity of Bile secreted in grammes, and of Sodium Taurocholate in decigrammes, at different hours after food.

Proportion and variation of pancreatic juice—
Thick unbroken line.

Bile in grammes—
Thick broken line.

Solids in pancreatic juice—%
Thin unbroken line.

Taurocholate of soda in decigrammes—
Thin broken line.



The diagrams have been drawn out to show the relations between the different digestive secretions, as regards time, and some of their constituents. In Chart i. the acidity values are derived from data given by the author (*cf. op. cit.*). In Chart ii. the curves for the amount of bile and of sodium taurocholate are based on figures by Hoppe-Seyler, and represent grammes and decigrammes respectively secreted by a dog every thirty minutes. The curve for the pancreatic secretion is only proportional; no definite amount is expressed, but the solids in the secretion are in percentage of the total.

of acid in the contents. In the case of dialysis, simple diffusion supplies the active agent. In the stomach diffusion may have some little part to play, but the vital processes in the cells of the acid-producing glands are much more nearly concerned. The different views taken of the actual formation of hydrochloric acid are detailed above (page 160), and do not concern us here. It appears to be most probable that there is what may be termed a "chemical reflex" at work. By that is meant the presence in the mucous membrane of the stomach of nerve fibrils possessing a power, probably through the ganglia in the stomach wall, of reflexly stimulating the secretory glands when food is introduced into the stomach; and that this power persists until there comes to be a definite percentage of free hydrochloric acid in the stomach contents. When this point is reached the nerve-terminations become irritated, and supply inhibitory impulses to the ganglia in place of accelerating messages. The presence of combined hydrochloric acid may be regarded as inert to a great extent as regards this mechanism, free acid being still poured out, although the total acidity of the contents be greater than would serve to arrest its secretion if the acid were all in the free state.

In man the natural percentage of free hydrochloric acid of the gastric juice may be regarded as the maximum possible under ordinary circumstances, although if much combined acid be present the maximum proportion of free acid is usually less. The natural total acidity is from .15 to .22 per cent., while the normal free hydrochloric acid after food, containing, as most foods do, a considerable quantity of proteid, is seldom more than .10 per cent., and may be lower. When carbo-hydrates alone are taken, the absence of proteids allows the free acid to reach its physiological maximum in a short time, and we find that this maximum is not exceeded unless the food be particularly irritating, or the gastric functions out of order. In the dog the maximum percentage of free hydrochloric acid permissible by our hypothetical mechanism is higher, .3 to .4 per cent. are not uncommon proportions in the stomach of this animal. Again, in those conditions in man in which excess of this acid in a free state is found, causing pain and discomfort, the nerves which act as regulators of the amount of free acid are unable to respond to the normal percentage of acid, and do not

arrest its secretion until an abnormal acidity obtains. The ordinary nerve-endings, sensible to pain, on the other hand, are irritated by the abnormal proportion of free hydrochloric acid, and notify the fact by representing it as discomfort and pain. The presence of free organic acids in the stomach contents would seem to irritate the sensory nerve-terminations almost as vigorously as that of hydrochloric acid; their influence on the mechanism for regulating the acidity is rendered more difficult to estimate owing to the fact that the organic acids, which take their origin in fermentation, can only occur in any quantity when the supply of free hydrochloric acid is deficient. They, in all probability, act on the nerve-endings after fermentation, owing to some diseased condition of the stomach walls, has begun, and diminish the stimuli sent to the secreting glands. Thus a temporary cause may bring about a prolonged deficiency of hydrochloric acid if the primary cause be neglected.

Another fact bearing on this question is the rapidity with which an alkaline solution introduced into the stomach is not only neutralised, but frequently rendered more acid than the normal contents from the increased stimulus given by the acid to the secretory glands; while acid solutions appear to become less acid if their acidity is above that of the normal stomach contents or juice, owing to dilution with a gastric fluid containing little or no acid.

Hitherto the influence of the central nervous system has been ignored in the discussion of this hypothesis. The fact that a flow of gastric juice has been observed in the dog (after the formation of a gastric fistula) at the mere sight of food, even when the saliva is prevented from reaching the stomach by the establishment of a salivary fistula, proves the existence of some communication by way of the brain between the nerves of sense and the gastric glands. Richet observed, in a patient with a gastric fistula, where the œsophagus was completely closed by a stricture, and not even saliva could reach the stomach, a copious secretion of gastric juice coincident with an increased flow of saliva, when savoury articles of food were chewed. Section of the pneumogastric nerves, however, has no effect on the secretion of gastric juice, although it arrests all movements of the walls of the stomach. The sympathetic nerves may also be cut without altering the secretion. We are forced to the conclusion by these facts that the local effects

depending on the presence of food are the chief agents at work; that the local mechanism stimulated by it, and probably by the products absorbed, is governed by the ganglia which are so numerous in the stomach walls; that it is possible that this mechanism includes a nerve arc for the regulation of the proportion of free acidity; and that the local centres can act independently of the central nervous system, but at the same time can be influenced by it on occasion.

If the existence be granted of a mechanism for preserving as far as possible under normal circumstances the maximum proportion of free mineral acid in the stomach contents proper to each individual after food of various kinds, it can easily be understood how the same proportion of free acid may prove irritating should the individual suffer from any disease in which the supply of nourishment to the stomach walls is deficient. For instance, women suffering from anæmia or chlorosis frequently complain of symptoms obviously due to the action of free hydrochloric acid, while examination of the stomach contents fails to reveal any excess, perhaps a slight diminution from the average amount. Here there is a proportional excess of acid, not a percentage above the average.

The secretion of saliva is governed entirely by a centre in the central nervous system, probably in the medulla, and the chemical reflex concerned with its reaction is not so apparent, nor, considering the short time during which it can act, so important. But here again the flow varies with the reaction of the food; after acids are taken into the mouth the rate of secretion is accelerated.

The pancreatic juice is practically secreted continuously though in varying quantities in dogs and man. Twenty-four hours elapse after a single meal before the flow ceases. In the rabbit, in *Herbivora*, and in *Ruminantia*, the flow is constant; in *Carnivora*, though practically constant, it varies in amount and in digestive activity with the time after, and the nature of, the food. The moment food enters the stomach the pancreatic juice begins to be secreted, but the rate of flow soon decreases until the chyme enters the duodenum, when a further increase occurs. The first flow is reflexly caused through the nervous system, the second in all probability by local stimulation to some extent at least. The fact that the contents of the stomach are acid stimulates the pancreas to neutralise it, while the constant presence in the bowel of organic acids pro-

duced by bacteria must serve to excite the gland to neutralise them, only with the result of further facilitating the growth of the organisms.

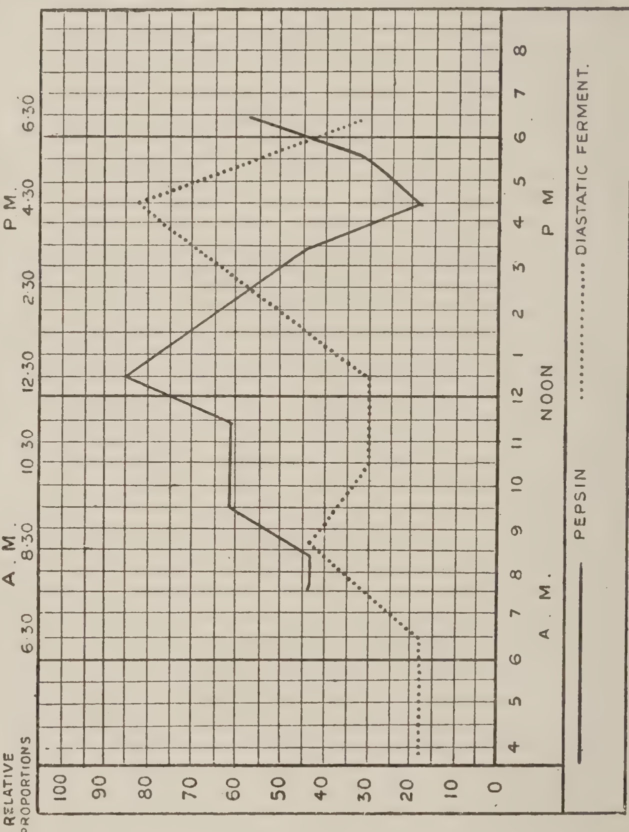


CHART V. (after Hoffmann).—Showing the Relative Amounts of (1) Pepsin and (2) Diastatic Ferment Excreted in the Urine at different hours of the day.

During the period of gastric digestion the passage of chlorine into the gastric glands, and its secretion as hydrochloric acid into the cavity of the stomach, render the blood more alkaline, the urine less acid. When the digestive process has been transferred to the intestine, *per contra*, the blood becomes less alkaline, the urine more acid. In the first period acid is practically withdrawn from the blood and passed out of the body, leaving organic and

alkaline salts of the bases previously combined with the chlorine. In the second period the chlorine is being reabsorbed as chloride of sodium, while alkali is passed out, the carbonate of sodium formed in the production of hydrochloric acid serving to re-form chloride of sodium; when secreted by the intestinal or pancreatic cells into the small intestine, it neutralises the acid coming from the stomach, and the base is again united to its former partner.

Some of the pepsin is absorbed by the walls of the stomach or intestine, or enters the blood-stream from the cells of the gastric glands without entering the stomach. The chart (Chart V.) shows the variations in the amounts of pepsin compared with those of the starch-converting ferment excreted in the urine at different periods of the day. The amount of pepsin increases till shortly after midday, diminishes until about half-past four, and then increases again as evening advances. The diastatic ferment, on the other hand, increases in amount up to half-past four, with a minor rise about 9 A.M.

The Digestion of Proteids by the Action of Acids aided by Pepsin.—The class of ferments which act on proteid bodies in an acid medium may be fitly represented by pepsin, the ferment of the animal stomach, and by hydrochloric acid, its coadjutor in its work.

For convenience, and in accordance with general custom, all proteolytic ferments which act only in an acid solution will be termed pepsin. Pepsin can aid all the mineral acids and many of the organic acids to digest proteids, but the digestive power of the different combinations varies greatly, and the strength of the acid necessary to produce the maximum amount of digestion also differs with each. In all probability, pepsin derived from different sources acts differently, though the variations in the process are as yet quite unknown. Wróblewski (*Ztsch. f. phys. Chem.*, xxi. s. 1) found that casein from cow's milk and fibrin were more easily and more completely digested by oxalic than by hydrochloric acid. He also obtained varying results from the digestion of a native proteid with acetic acid and pepsin made from different animals. In carnivorous plants the acid present invariably belongs to the fatty series, and is generally formic acid, either alone or along with other acids. In the *Protozoa*, in whom digestion is intracellular, the reaction of the protoplasm before proteid food has been engulfed is alkaline. Immediately after the entrance of any proteid-containing body within the cell the reaction of its contents becomes acid. Greenwood and Saunders found that *Amœbæ* changed the colour of litmus, alizarin, congo red, etc., from that representative of an alkaline reaction to that of acid

conditions when fed with bodies impregnated with these stains. If the body was indigestible it was extruded and the reaction of the cell again became alkaline. If digestible, as soon as it was dissolved, the alkaline reaction returned. The acid secreted is unknown, but the necessary ferment is probably akin to the pepsin of higher organisms.

Although hydrochloric acid possesses the greatest power among acids of bringing about peptic digestion, the power of several others is by no means small. Thoyer gives (*Mém. de la Soc. de Biol.*, February 20, 1891) a list of acids arranged in their order of digestive power—

1. Hydrochloric acid.
2. Sulphuric acid.
3. Acetic acid.
4. Oxalic acid.
5. Tartaric acid.
6. Citric acid.
7. Lactic acid.
8. Hydrofluoric acid.

On the other hand, Hubner (*Fortschritte des Med.*, xxii. s. 163, 1894) arranges the digestive power of the halogen acids exactly in inverse order to their molecular weights, hydrofluoric first, hydrochloric next, hydrobromic third, and hydriodic last and least powerful—

Acid.		Molecular Weight.
1. HFl.	=	20.0
2. HCl.	=	36.5
3. HBr.	=	80.0
4. HI.	=	128.0

TABLE XXVIII.—THE RELATIVE ACTION OF PEPSIN ON EGG ALBUMIN IN THE PRESENCE OF VARIOUS ACIDS.

I.—*Duration of Digestion 2½ hours at 38° Cent.*

Acid.	Acidity per Cent. as HCl.	Percentage of Albumin rendered uncoagulable.
1. Oxalic Acid	.15	63 3
2. Hydrochloric	.146	47.7
3. Trichloracetic	.036	41.1
4. Nitric	.169	34 4
5. Sulphuric	.146	33.3
6. Citric	.139	30.0
7. Phospho-wolframic ...	.003	0
8. Benzoic	.0584	0
9. Sulphanilic	.0438	0
10. Acetic	.21	0

II.—*The same Acids added to a Solution of Egg Albumin, Pepsin, and Hydrochloric Acid. Duration of Digestion* 15 *hours at* 38° *Cent.*

Acid added.	Total Acidity.	Acidity due to HCl.	Per cent. as HCl not due to HCl.	Proportion of HCl to Acid.	Albumin Digested per cent.
1. Sulphuric . . .	.31	.1014	.2086	1—2.05	97.7
2. Acetic . . .	.48	.192	.288	1—1.5	95.5
3. Sulphanilic . .	.16	.1014	.0586	0.579—1	91.1
4. Benzoic . . .	.18	.1014	.0786	0.77—1	84.4
5. Hydrochloric . .	.115	.115	.0	....	82.2
6. Nitric . . .	.44	.1825	.2575	1—1.4	71.1
7. Trichloracetic . .	.238	.152	.086	0.56—1	57.7
8. Citric	.25	.114	.136	1—1.19	53.3
9. Oxalic . . .	.233	.1014	.1216	1—1.19	44.4
10. Phospho-wolframic .	.15	.1014	.0486	0.479—1	0

Table XXVIII. gives the results of a series of experiments upon the relative proteolytic action of pepsin in the presence of various acids on egg-albumin, alone and when added to a solution containing hydrochloric acid of constant amount, though the mixtures were not of constant proportional acidity value after their addition to the acid solutions. In each case a known quantity of egg-albumin was used, and after the expiry of the experiment the weight of the coagulable remainder determined. As the formation of acid-albumin may be regarded as the preliminary stage of proteolysis, this body was not separated from the lower proteid derivatives. From the first part of the table it is seen that the greatest loss of albumin after digestion for two and a half hours occurred in the experiment in which oxalic acid was used. Hydrochloric acid of 0.146 per cent. caused the second greatest loss, closely followed by 0.036 per cent. trichloracetic acid with 41.1 per cent. uncoagulable. The result obtained from trichloracetic acid was always entirely due to the amount of acid-albumin formed. Nitric and sulphuric acid were almost of the same activity, and were followed at a little distance by citric acid. The other acids tested had no action. The position occupied by oxalic acid corroborates Wróblewski's observations, already noted, on the peptic digestion of fibrin.

The results depicted in the second part show that the power of individual acids of digesting albumin bears little relation to their action on the proteolysis occasioned by

pepsin-hydrochloric acid. The addition of sulphuric, acetic, sulphanilic, and benzoic acids rather increased the action of hydrochloric acid and pepsin. The presence of the others diminished it, notably oxalic acid with only 44.4 per cent. of albumin altered after fifteen hours, and phospho-wolframic acid, which arrested all digestive action.

Although the action of pepsin, whereby an acid is able to act on proteid molecules, is exceedingly obscure, the action of the acid facilitated by pepsin is better known, but even this knowledge is by no means based on a sound footing.

The changes which occur in the intimate chemistry of the large composite molecules of native proteids, when subjected to the action of hydrochloric acid and pepsin, must now be considered in some detail, as they constitute some of the most important features in the natural history of digestion. Their action on egg-albumin may be taken as the general type of the changes caused by them in all proteid bodies.

If the whites of several eggs be taken and freed from their fibrous shreds by clipping with scissors, shaking up with small bits of broken glass, and filtering through muslin, the globulin and alkali-albumin in the filtrate may be removed by cautiously adding a small quantity of dilute hydrochloric acid and catching the resulting precipitate on a filter-paper. The further filtrate must now be carefully neutralised by the addition of a weak alkali, and any precipitate which may appear during the process again filtered off. The clear neutral fluid left may be still further purified by dialysis into distilled water to remove the salts. We have now a solution of egg-albumin in water, practically in as pure a state as is possible without proceeding to very elaborate methods. If a dilute solution of hydrochloric acid be added to this fluid, and the fluid tested from time to time, an increasing amount of acid-albumin will be found to be present, and, until a certain proportion of acid has been added, no trace of free hydrochloric acid can be discovered; until, indeed, as much acid has combined with the albumin to form acid-albumin as is required. Whenever the proportion of acid by weight reaches about 8-9 per cent. of the albumin in the solution, the further addition of it at once appears as free volatile acid. The addition of more acid brings about no further change in the proteid.

The action of dilute acids in the cold transforms albumin into acid-albumin, but goes no further.

If a small quantity of pepsin be added to the solution of egg-albumin at the same time as the hydrochloric acid, the resulting change goes much beyond that caused by the acid alone. Acid-albumin is to be looked upon as a molecule of albumin in which some of the water-molecules attached to it have been replaced by molecules of acid. It should be mentioned here that prolonged action of dilute hydrochloric acid (0.25 per cent.) at 40° C., boiling with sulphuric acid (3-5 per cent.), or the prolonged action of dilute acid with an inadequate quantity of pepsin, converts the acid-albumin into—first, anti-albuminate, a variant of acid-albumin which cannot be further digested by acid and pepsin; and secondly, transforms another portion into albumoses and peptones.

The changes which follow the formation of acid-albumin in the ordinary course of gastric digestion consist primarily in the splitting up of the acid-albumin into smaller and more hydrated molecules. In the presence of pepsin the acid is enabled to cleave the unstable and unwieldy parent molecule, already combined with as many molecules of hydrochloric acid as it can retain in the absence of pepsin, into smaller molecules, each with a greater affinity for the acid, and, when the acid has been removed, containing more of the elements of water. These smaller proteid molecules are acted on by the acid in a precisely similar manner, yield still more hydrated and less bulky molecules, while these in turn suffer the same fate until the limit of acid and peptic digestion is reached by the formation of peptones.

The process may be represented by this schema—

TABLE XXIX.

ALBUMIN
|
ACID-ALBUMIN

Proto-albumose.	Hetero-albumose.
Deutero-albumose.	Deutero-albumose.
Peptone.	Peptone.

Kühne and Chittenden have proved, however, that the process is by no means as simple a one as represented in this schema. They have shown that in all *artificial* digestion

experiments two groups of very similar bodies are formed, the one, which is composed of more stable substances, they term the anti-group, the other, less resistive to hydrolytic agents, the hemi-group. A modification of their scheme is as follows:—

TABLE XXX.

ALBUMIN

ACID-ALBUMIN

Anti-albumose. — Hemi-albumose.

Anti-peptone. — Anti-peptone. — Hemi-peptone. — Hemi-peptone.

AMPHO-PEPTONE.

Consideration of the "Anti" compounds would lead us too far afield, and will be omitted.

The percentage composition of different derivatives is practically the same as that of the original proteid. But they cannot be the same in reality. Their properties are very dissimilar, and all point to the lower members of the series having a smaller molecule than the members above them. The different bodies derived from albumin are more soluble in various menstrua, more easily diffusible, and less easily precipitated by alcohol and other reagents as we go down the scale. Their compounds with acids and metals contain a greater proportion of these bodies than the compounds of those above them.

The evidence in support of a series of proteid bodies as the result of peptic digestion, presenting a progressive diminution in the size of the molecules, though it may be insufficient for the purpose of estimating their exact size, is extensive and conclusive enough to enable us to hazard a surmise as to their relative bulk. Both native and derived proteids form compounds with acids and with salts of the heavy metals. If these compounds be analysed, the lower down the proteid scale the higher is the proportion of acid or metal in the salt. These compounds of proteids with acids and metals are by no means uniform bodies, the strength of the reagents used, and the temperature at which the reaction takes place, cause variations in the products. Thus Harnack (*Zeitschrift f. phys. Ch.*, Bd. v., s. 198) obtained two compounds of egg-albumin and copper, in which the copper was as 1.35 per cent. or 2.64 per cent. to the albumin. The composition of the albumin remained the same in both. So in the analogous silver compounds Loew (*Arch. f. Phys.*, Bd. xxxi., s. 393) could vary the

amount of silver present in his albuminate of silver by altering the strength of his solutions. If strong solutions of silver nitrate, copper sulphate, gold chloride, mercuric chloride, and other metallic salts, be added in excess to solutions of proteids a precipitate forms, which is as a rule flocculent and lighter in the case of the native albumins, finer and heavier in the lower derivatives. The colour of the lower compounds is usually more pronounced than that of the higher.

The proportions between the amounts of the different proteids and of hydrochloric acid in their combinations are of great interest. The writer has performed a number of experiments intended to determine the relationship between this acid and various proteid bodies, with fairly constant results. The variations, however, are sufficiently large to suggest that our present methods of separating proteids from one another are very incomplete, and that in all probability the broad distinctions of the simpler proteids serve to cover a much more numerous series of these bodies, distinct from one another yet differing only in minute details.

The usual method by which proto-albumose is separated from deutero-albumose by saturating the solution containing them with chloride of sodium, if carried out in stages yields at least three if not four precipitates answering to the general tests for proto-albumose, but giving slightly different reactions. Thus, if a solution containing both of these albumoses be evaporated after the addition of chloride of sodium, before absolute saturation is reached a precipitate appears in masses, floating on the surface of the water, or adhering to the sides of the vessel. After filtering this off and evaporating further until crystals of the chloride begin to form, a further portion of the proteid can be removed. Continued heating of the second filtrate to facilitate the removal of the excess of salt yields a further crop, and sometimes a fourth crop may be obtained before all the primary albumoses have been isolated. From each of these precipitates some hetero-albumose can be separated by the action of dialysis.

The four substances were found, after purifying, to present certain points of difference; the series gradually became more akin to the secondary group. Thus the precipitate formed on the addition of chloride of platinum to a watery solution of the first was light yellow in colour, insoluble in cold water and hardly soluble in boiling water; of the second, was darker in colour, and only slightly soluble in hot water; of the third, large and flocculent masses, yellow in colour, and soluble in cold water but more readily in hot water; while the precipitate occasionally obtained after this formed darker and finer flocculi which were very soluble in water, in alcohol up to 70 per cent. but insoluble in ether. The first two precipitates appeared to be able to combine with from 9-10 per cent. of hydrochloric acid, the third with 13 per cent., and the last with about 14 per cent.

Pekelharing has described two precipitates obtainable, after removal of the primary and secondary albumoses by the saturation of their solutions with ammonium sulphate, first slightly acidifying and making sure that the fluid has been thoroughly saturated with the salt at the boiling point. If, after the precipitated albumoses are filtered off, the filtrate be further concentrated so that when at the boiling point a portion of the ammonium sulphate remains crystalline, be then rendered alkaline with ammonia and allowed to cool, a deposit of small particles of proteid gradually forms. In some instances, after filtering this and treating the filtrate in a similar manner, but with the addition of acetic acid, a further precipitate can be obtained. Any

proteid substance remaining after this may be regarded as of the nature of pure peptone, but it is not improbable that in time further members of the long series dividing true peptone from native proteid will be discovered.

The alterations which occur in the highly complicated albumin molecule before it becomes, it may be only in part, the very much simpler though still complex peptone molecule through the action of dilute acid or alkali, and ferments, possibly consist of a continued and lengthy series of small changes similar to but much more numerous than those which intervene between a molecule of starch and a molecule of maltose, changes which together result in an alteration in chemical relations, and remain at present beyond the power of the chemist to appreciate. All determinations of the chemical composition and reactions of proteid bodies have hitherto yielded very varying results, not only because of the difficulty experienced in freeing them of salts, as has been already mentioned, but also because, except in the case of the artificial crystalline globulins, there is no doubt but that few analyses have been performed on any class of proteid absolutely free from proteids of another group, or belonging to contiguous members, in the proteid series. So many analyses, however, have been carried out on the different and larger groups that their mean may be taken as conveying a fair estimate of the average composition of each group, and probably may be regarded as the actual composition of the individual proteid body which occupies the position midway between the lowest member of the group immediately above, and the highest member of that below the group in question. If, therefore, proto-albumose really includes four or more different bodies, all of which differ from the deutero-albumoses, for instance, in that they are insoluble in hot saturated solutions of sodium chloride, and are precipitated by trichloracetic acid, the values obtained for proto-albumose as an entity will represent the average values for its individual members. The average percentage of hydrochloric acid which the writer has found to combine with proto-albumose is from 11 to 12; the figures obtained from the four separate precipitates yield a mean of 11.5 per cent.; while the highest member gives a figure close to that of acid-albumin, the lowest one is only slightly removed from that obtained from deutero-albumose.

Blum has laid it down that the percentage of hydrochloric acid which

can combine with the series of proteid bodies formed during digestion increases as the proteids decrease in size and complexity.

Gurber, on the other hand, by estimating the nitrogen of such compounds by Kjeldahl's process, and the hydrochloric acid with Günzberg's reaction, found that acid-albumin gave 1 molecule of hydrochloric acid to 5 atoms of nitrogen, or if nitrogen be taken as 15 per cent. of the albumin, the acid formed about 7 per cent. of the compound by weight; that, similarly, proto-albumose combined with only 4 per cent. of the acid; while deutero-albumose united with about 10 per cent., and peptone with 8 per cent. of the acid. Nitrogen estimations, however, of bodies obtained through the use of ammonium salts are seldom trustworthy, owing to the great difficulty attendant on the complete removal of ammonia, and the consequent fallacy introduced into the nitrogen values.

Cohnheim has also determined the proportion of hydrochloric acid which combines with the various proteids. He only used albumoses and peptone in his experiments. He found—

Proto-albumose	combined with	4.3	per cent.	hydrochloric acid.
Deutero-albumose	,,	5.5	,,	,,
Hetero-albumose	,,	8.2	,,	,,
Anti-peptone	,,	16.0	,,	,,

The proportion between the figures for proto-albumose and those for deutero-albumose, though they are actually smaller, is the same as between those obtained by the author, while the percentage of acid combining with peptone is in both series much above the percentage combining with the other proteids.

The author, by drying solutions containing known quantities of different proteids after the addition of hydrochloric acid, and by checking the results obtained by the use of Günzberg's reagent for determining the exact moment at which, with the addition of a deci-normal solution of the acid drop by drop to similar solutions, free hydrochloric acid could be detected, obtained the following results :—

TABLE XXXI.—*Percentage of Hydrochloric Acid in its Compounds with Proteids.*

(Expressed in terms of HCl per cent. of total.)

Proteid.	HCl per cent.
Egg-albumin	0—8
Serum-albumin	0—9
Serum-globulin	0—10
Acid-albumin	8—9
Hetero-albumose	8.84
Dys-albumose	12.1
Proto-albumose	11—12
Deutero-albumose	13—14
Peptone	19—20

An albumin molecule does not appear to lose its characteristic properties until 8 or 9 per cent. of hydrochloric acid has com-

bined with it, when it affords the reactions of an acid-albumin. Hetero-albumose corresponds very closely to acid-albumin in its reactions, and combines with the same amount of acid. The other proteid derivatives combine with more of the acid as they become simpler in character.[1]

The size of the various proteid molecules may be suggested by the percentage of the metal present in these compounds. In considering this question it must be remembered that the metals are combined in the form of their salts. Thus when silver nitrate is used to precipitate proteids the resulting compound is formed by the proteid and the actual silver salt. The percentage of metallic silver recovered by incineration refers therefore to the weight of the total compound, not of the proteid and silver alone. The hydrochloric acid compound is similarly a hydrochloride, not a chloride; while the chlorides of gold and of platinum, and the sulphate of copper form integral parts of the precipitates. The doubtful point is the behaviour of the molecules of water. Probably molecules of native proteids coagulated by these reagents lose all their water, while it is also probable that the compounds of the lower proteids with metallic salts retain part of their attached water molecules, as they are much more soluble in warm, and some even in cold water. The hydrochloric acid molecules may be regarded as ousting a similar number of water molecules attached to the proteid without disturbing the remainder of the water molecules, unless it be present in strong solution sufficient either to coagulate albumin or split it and other proteids into non-proteid derivatives.

Drechsel (*Journ. f. prakt. Chem.*, N. F. Bd. 19, s. 331) analysed a crystalline compound of a vegetable globulin with magnesium oxide, and found 1.43 per cent. of the metallic oxide in it when dried at 110° Cent. This gives the molecular weight of the proteid present as 2757. A similar sodium compound gave a weight of 1496. Harnack's copper albumin, with 1.35 per cent. of copper, affords an albumin-molecule weighing 4576, or a little more than three times that of the sodium preparation; his second copper compound with 2.64 per cent. of copper yields a proteid molecule of 2266, or just one-half of the first. Similarly, Loew's (*Pflüger's Archiv.*, Bd. 31, s. 393) silver compounds with 2.3 per cent. and 4 3 per cent. of silver, correspond to 4587 and 2403 respectively.

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[1] Paal (*Bericht. d. d. Chem. Ges.*, xxvii., s. 1827) has obtained compounds of albumoses and peptones with hydrochloric acid containing from 2.2 to 19.88 per cent. of the acid, with molecular weights ranging inversely to the proportion of acid, from 252 to 2120.

CHAPTER VIII.

Digestive Processes (*continued*).

The passage of the food from the Stomach into the Duodenum—Intestinal Digestion — The Pancreatic Secretion — Historical — Characters — Ferments—Action on Proteids—The Liver—Bile—Other actions of the Liver—Digestion in the Small Intestine—Reaction of the contents —Absorption of fluids—Digestion in the Large Intestine.

The Passage of the Chyme from the Stomach into the Duodenum.—Up to recent years it was believed that, at the end of gastric digestion, the contents of the stomach were rapidly discharged almost *en masse* into the bowel. From the observations, however, of Cahn and von Mering on the dog by means of duodenal fistulæ, it is clear that some of the stomach contents are propelled into the bowel shortly after food has been taken. For instance, these observers found that after the animal drank plain water fluid began to escape from the stomach in a few minutes. When the dog was given solutions of various substances in water, such as alcohol, peptones, and albumin, as much fluid, and often more, was discharged through the pylorus as had been taken; while the peptones and the alcohol were found to be diminished in amount. That is to say, that while it has little or no power of absorbing water, the stomach is able to absorb a considerable quantity of such substances as peptone and alcohol. Unfortunately, they did not investigate the conditions under which the stomach contents are discharged after a meal of mixed fluids and solids.

Schüle (*Zeit. f. Klin. Med.*, xxviii., p. 87) found in a dog with a similar duodenal fistula that the temperature of the food given had a great influence on the time when the stomach emptied. Thus 300 c.c. of water at 18° C. were passed through the pylorus in 10 minutes, a physiological salt solution at the same temperature in 21 minutes. The same amount of water at 28° C. and at 40° C. passed through in less than 10 minutes, while at 0° C. 15 minutes elapsed before the first portion appeared. If milk were given instead of water the stomach emptied almost as quickly, while after solids were given the pyloric discharge was delayed, and after both fluids and solids, the fluids passed through first. The greater the amount of fluid

taken with a meal the sooner a portion of the food was propelled through the pyloric orifice. (Chart VI.)

As a general rule, in man and in the dog we may look upon one hour as the usual time at which, after an ordinary meal of mixed fluids and solids, the first portion of the gastric contents passes through the pyloric orifice. The process goes on for a considerable time, the pylorus opening in a rhythmical manner every five to ten minutes until all the stomach contents have been passed through. The larger the meal and the more solid the contents, the longer does this process take. Of all the bodies which make up the food fats are the last to leave the stomach, principally because, owing to their lower specific gravity, they float on the surface.

The Pancreatic Secretion.—The data which we possess concerning the nature and the secretion of the pancreatic juice have been largely derived from observations made upon animals. This is not the place to give a description of pancreatic fistulæ, and of the various methods employed for their formation. De Graaf, in 1664, was the first to make a successful fistula, but it was not until 1849, when Claude Bernard established pancreatic fistulæ in dogs, that the secretion obtained was studied with any care. Heidenhain, Ludwig, Weismann, and Bernstein are some of the later observers in this subject; while Colin, by means of pancreatic fistulæ in large ruminants, was enabled to obtain large quantities of fluid, and thereby to facilitate the investigation into its composition. Unfortunately the pancreatic juice flowing from a permanent fistula soon loses its normal characters; for a day or two it may be regarded as normal, but afterwards it increases in quantity while the solids contained in it decrease in amount.

The facts which have been substantiated go to show that if food be withheld for twenty-four hours or longer the secretion of the gland ceases. If food be now given the juice is at once poured out in increasing amount (Chart IV.) for the first three hours. From this hour until the fifth or seventh the rate of flow diminishes, not to increase again until the ninth or eleventh hour. After this a gradual diminution takes place in the rate, until at the seventeenth hour little fluid is secreted, and at the twenty-fourth hour the secretion ceases entirely. The character of the pancreatic juice secreted during the earlier hours of digestion differs from that poured out later. At first

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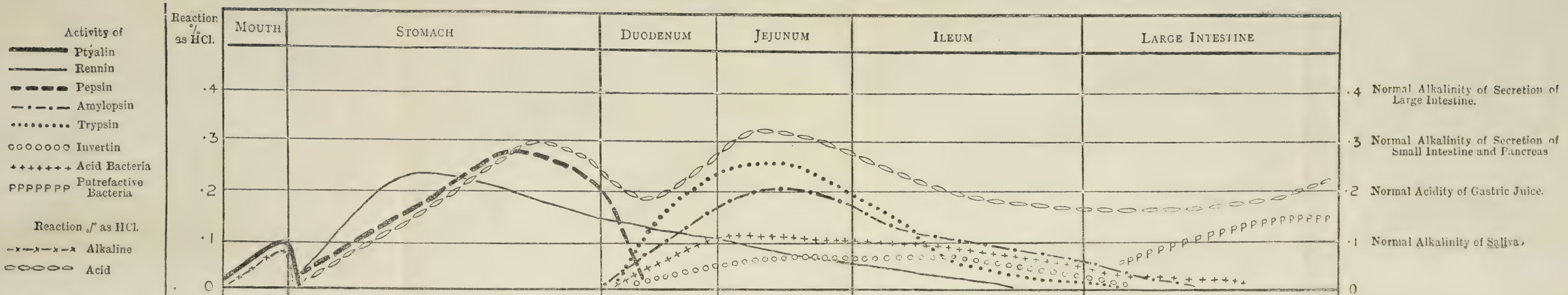
CHART VI.—Illustrating the Spheres of Activity of the different Ferments, and the probable reaction of the contents in each section.



	Mouth	Stomach	Duodenum	Jejunum	Ileum	Large Intestine
Reaction of Contents	Alkaline or Acid	Acid	Acid or Neutral	Acid	Acid	Acid
Reaction of Secretion	Alkaline	Acid	Alkaline	Alkaline	Alkaline	Alkaline
Ferments Acting	Ptyalin	Pepsin, Milk-Curdling	Trypsin Milk-Curdling Fat-Splitting Fat-Emulsifying Amylopsin Invertin	Trypsin Milk-Curdling Fat-Splitting Fat-Emulsifying Amylopsin Invertin	Trypsin Amylopsin Invertin Fat-Splitting Bacteria of Fermentation	Bacteria of Putrefaction; the ferments from the small intestine still slightly active in the upper part.
Portion of Tract	Mouth	Stomach	Duodenum	Jejunum	Ileum	Large Intestine
Chief Actions	Starch Conversion into Maltose	Proteolytic Milk-Curdling Inversion of Sugar by HCl. Absorption of Alcohol, peptone, etc.; none of water Antiseptic	Proteolytic Fat-Splitting. Conversion of Starch into Maltose (Amylopsin), and Maltose into Dextrose and Lævulose (Invertin); formation of antiseptic acids by Bacteria			
			Absorption considerable	Absorption moderate	Absorption slight	Absorption great

In this Chart an attempt is made to epitomise the chief features of digestion in the whole alimentary tract of man graphically and descriptively. The curves show the average limits of the activity of each ferment in a relative manner, and the degree of acidity or alkalinity in turn of hydrochloric acid per cent. in each section of the tract. The reaction values are not given as absolute, while the normal values added on the right are those midway between the extreme values for each often found in health. The duration of stay in each part is very variable—half minute in the mouth, six seconds during deglutition, two to five hours in the stomach, from the second to the sixth or twenty-third hour in the small bowel, and from the sixth to the twenty-fourth hour or longer in the large intestine.

it is viscid, gelatinises on cooling, and coagulates easily; as digestion proceeds it becomes less viscid, more dilute, and sparingly coagulable. The changes in the cells of the gland before and during active secretion are described in connection with its proteolytic ferment, trypsin, and the zymogen, trypsinogen. The pancreatic juice, unlike the saliva, is secreted at a low pressure—in fact, its pressure only reaches about $\frac{1}{10}$ of that of the saliva, or below 20 mm. of mercury.

Quantity.—Owing to the alterations in the flow of the juice shortly after the establishment of a pancreatic fistula, as mentioned above, the estimation of the normal quantity is beset with difficulties. Observations, however, upon animals serve to show that there is no ratio between the size of the gland and the amount of secretion. The following table shows the quantity per kilogramme of body-weight secreted in the twenty-four hours, as determined by Colin :—

TABLE XXXII.—*Rate and Proportional Secretion of Pancreatic Juice.*

	Weight of Pancreas.	Secretion per Kilo. in 24 hours.	Maximum Secretion per hour.
	Grammes.	Grammes.	Grammes.
Man	88	3.01-5.0	—
Dog	—	2.4	9.1-20.8
Horse	300	16.8	265
Cow	300	14.4	200-270
Sheep	50-60	12.0	8
Hog	140-180	7.2	15

TABLE XXXIII.—*Composition of Pancreatic Juice.*

	DOG. (Schmidt.)		HORSE. (Hoppe-Seyler.)
	1. Immediately after Operation.	2. Permanent Fistula.	
Water	900.76	980.45	982 50
Total Solids	99 24	19 55	17.50
Organic Solids	90 44	12 71	8 88
Ash	8.80	6.84	8.62
Na (Sodium)	0.58	3.31	—
Chlorides	7.37	3.43	—
Phosphates	7.73	0 09	—
Mg (Magnesium)	0.12	0.01	—

Pancreatic juice is alkaline in reaction, equal to about 0.3 per cent. NaHO, with the high specific gravity, when obtained from a recent fistula, of 1030, but falling to 1010 in course of time (see Table XXXIII.). It coagulates on heating into a firm white mass, from which an alkaline opalescent fluid separates out containing alkali-albumin. When dropped into water a precipitate forms which is soluble in solutions of sodium chloride or dilute acids; a similar precipitate is formed if it is dropped into dilute acid solutions, but clears up on agitation of the fluid. An abundant white precipitate follows the addition of alcohol, which is largely soluble in water, and not reprecipitated by acetic acid until its action has continued for some time. The alcoholic precipitate contains, or carries down with it, the different pancreatic ferments. Pancreatic juice readily undergoes putrefaction, yielding the red reaction with chlorine water indicative of tryptophan during the earlier stages of this process, and, after this reaction has disappeared, the red colour formed by indol when impure nitric acid is added.

Pancreatic Ferments.—Three ferments are undoubtedly present in pancreatic juice.

1. Trypsin; proteolytic in neutral, faintly alkaline or acid (where the acidity is not due to mineral acids) media, and able to decompose proteids into amido-acids as well as into peptones.
2. Amylopsin; a diastatic ferment, acting similarly to ptyalin.
3. A fat-decomposing ferment, steapsin, forming glycerine and fatty acids by hydrolysis from neutral fats.

A fourth is probably present in the form of a milk-curdling ferment, and still another is hypothetically assumed to be contained in pancreatic secretion and to act not upon the actual intestinal processes so much as upon the activity of glycogenesis or glycolysis in the liver and body generally. A fat-emulsifying ferment was formerly thought to be present by Claude Bernard, but this view has been shown to be erroneous. The emulsification of fats by the pancreatic juice is probably brought about by the carbonate of sodium and the proteids contained in it.

Digestion of Proteids by Trypsin.—Trypsin acts energetically on albumins and globulins in a 1 per cent. solution of sodium

carbonate and at a temperature of 40° C. For the accurate observation of the changes brought about by the ferment, the mixture must be rendered aseptic by the addition of a small quantity of salicylic acid or thymol. Fibrin digested by trypsin does not swell up as in peptic proteolysis, but its edges are gradually eroded away, until there remains nothing save a powdery residue. The first products of tryptic proteolysis are identical with those resulting from the action of pepsin and acids; hemi-albumose and anti-albumose are formed, to be changed in turn into hemi- and anti-peptone. Further action transforms the hemi-peptone into such amido-acids as leucin, tyrosin, and glutamic acid. Kühne found that of 382 grammes of dried fibrin, with 55 grammes of pancreas (15.2 grammes when dried), 343.7 grammes was dissolved, yielding 211.2 grammes of albumoses and peptones, 13.3 grammes of tyrosin, and 31.6 grammes of leucin. (Table XXXIV.)

TABLE XXXIV.—*The Digestion of Fibrin by Trypsin.*

Dried fibrin and gland tissue	397.2 grammes.
Dissolved	343.7 ,,
Unaffected	53.5 ,,

Peptone and albumoses	211.2 grammes	= 53.1 per cent.
Tyrosin	13.3 ,,	= 3.3 ,,
Leucin	31.6 ,,	= 7.9 ,,
Other soluble products	87.6 ,,	= 22.0 ,,
Unaltered	53.5 ,,	= 13.7 ,,

Tryptic proteolysis, in the absence of bacteria, is unaccompanied by the evolution of gases. Hüfner found, indeed, that oxygen was absorbed, while carbonic acid gas was developed, but in very minute quantity. In Kühne's experiment the albumoses and anti-peptones were not individually separated from each other. In another observation this observer, along with Chittenden, obtained 120 grammes of pure anti-peptone from 300 grammes of fibrin, or 40 per cent. The amido-acids resulting from the action of trypsin on proteids in the absence of bacteria are bodies in which an atom of hydrogen contained in the alcohol-radical of various acids is replaced by amidogen. (Table XXXV.)

Thus acetic acid, CH_3COOH, becomes $CH_2(NH_2)COOH$, or glycocoll; and caproic acid, $C_5H_{11}COOH$, becomes $C_5H_{10}(NH_2)COOH$, or leucin.

TABLE XXXV.—*The Products of the Action of Trypsin on Proteid Substances,* (A) *in the absence of Bacteria;* (B) *with Bacteria present.*

A.

Native Proteid.

Albuminat (alkali-albumin).
Anti-albumose.
Proto-albumose. Deutero-albumose.
Hetero-albumose.
Deutero-albumose. Anti-peptone.
Anti-peptone.

Alkali-albumin.
Hemi-albumose.
Proto-albumose. Hetero-albumose. Deutero-albumose.
Deutero-albumose. Deutero-albumose.
Hemi-peptone. Hemi-peptone. Hemi-peptone.

Amido-acids.
Leucin.
Asparagin.
Glutamic acid.
Amido-valerianic acid
(Butalanin).

Bases.
Lysin.
Lysatinin.
NH_3.

Pigment.
Tryptophan.

Aromatic body.
Tyrosin.

B.

1. Native Proteid.
Albumoses.
Peptone.

Amido-acids.

Fatty acids.
Lactic { active.
inactive.
Acetic.
Butyric.
Succinic.

Indol.
Skatol.

Tyrosin.
Parakresol.
Phenol.

Leucin has, however, been shown to correspond in character and properties more closely to amido-isobutyl-acetic acid, an isomer of amido-caproic acid. Tyrosin is a para-oxyphenyl-amido-propionic acid, or

$$HO.C_6H_4.CH_2.CH(NH_2)CO.OH + H_2.$$

Asparagin is amido-succinic acid, and glutamic acid amido-pyrotartaric acid.

When the remaining proteids and all the amido-acids have been removed from a solution which has undergone tryptic digestion in the absence of bacteria, at least 30 per cent. of the original proteid remains unaccounted for, as shown by the deficit in the nitrogen contained in the substances obtained. Arguing from this that some products of a different kind must be formed containing the missing nitrogen, Drechsel investigated the mother-liquor left after the removal of the amido-acids, and succeeded in isolating two basic bodies, lysin and lysatinin. Lysin is a diamido-caproic acid, in which two atoms of hydrogen are replaced by amidogen.

$$C_5H_{11}COOH = C_5H_9(NH_2)_2COOH = C_6H_{14}N_2O_2.$$

Lysatinin ($C_6H_{11}N_3O$) is analogous to creatinin in composition, but may be regarded as a creatin if a molecule of water be not looked upon as water of crystallisation; $C_6H_{13}N_3O_2$, or lysatinin. Another base, ammonia, is formed at the same time from the proteid-molecules acted on. The xanthin bases are not produced by the aseptic digestion of simple proteids by trypsin, but, as Kossel has shown, are derived from the nucleins present along with the proteids. The importance of the discovery of lysatinin lies chiefly in the fact, subsequently obtained by Drechsel, that urea can be formed from it by simple decomposition. By a process of decomposition, not oxidation, the proteid molecule can yield lysatinin, and further decomposition affords urea. The amount of urea which can be obtained from lysatinin only represents one-ninth of that represented in the original proteid from which it has been formed. Schützenberger obtained 2.79 parts of carbonic acid from 100 parts of dry albumin. One molecule of lysatinin when decomposed yields one molecule of urea, and finally one of carbonic acid. Thus 2.79 grammes of CO_2 may arise from 8.95 grammes of lysatinin, or from the 3.8 grammes of urea formed from it. Each 100 grammes of proteid corresponds to 34.3 grammes of urea, 3.8 grammes of which can be obtained by way of lysatinin, or one-ninth of the whole.

The Functions of the Liver.—Bile.—The actions of the liver cells upon glycogen and in the formation of urea will be fully dealt with under metabolism. The influence of the biliary excretion upon intestinal digestion may be shortly noted, along with some facts concerning its physical properties.

Table XXXVI. gives the percentage composition of bile in man and various animals.

The amount of bile formed *per diem* in man is about 800 to 900 grammes, containing 14 to 15 grammes of solid material,

TABLE XXXVI.—*Mean Percentage Result of Analyses of Bile in Man and various Animals.*

Constituents.	MAN. Bile from Gall Bladder.			MAN. From Fistula.	DOG. Gall Bladder.	DOG. Fistula.	Ox.	Pig.	Kangaroo.	Goose.	Python.
Mucin and Pigments ..	2.0	2.32	1.43	0.228	0.454	0.053	0.30	0.59	4.34	2.56 / 3.1	0.89
Lecithin	—	—	0.53	0.005	2.692	0.118					
Cholesterin	0.5	0.21	0.35	0.0514	0.449	0.074		1.12	0.59	0.36 / 0.3	0.03
Fats	1.2	0.42	0.73	0.0103	2.841	0.335	8.00				
Soaps		—	1.39	0.118	3.155	0.127					
Taurocholate of Soda ..	7.5	0.968	0.87	0.052	11.959	3.460		8.38	7.59	14.96 / 16.4	8.46
Glycocholate of Soda ..			3.03	0.642	—	—	—		—		
Inorganic Salts	0.8	0.78	—	0.641	0.199	0.408	1.26	1.01	0.5	2.10 / 2.6	0.2
Chlorides	—	0.25	—	0.598	0.015	0.185	—	—	—		
Sulphates	—	—	—	—	0.054	0.068	—	—	—		
Phosphates	—	0.41	—	—	0.097	0.06	—	—	—		
Carbonates	—	—	—	—	0.024	0.086	—	—	—		
Total Solids	12.0	14.0	—	1.747	—	—	9.56	11.20	14.13	19.98 / 22.4	9.58
Water	88	86.0	—	98.253	—	—	90.44	88.8	85.87	80.2 / 77.6	90.42

a small quantity when the size of the liver—1400 to 1600 grammes—is considered, the more disproportionate to its volume when the numerous functions performed by the organ are remembered. The ratio between the quantity of bile secreted and the body weight reaches from 12 to 17 c. cm. to each kilogramme, or from 0.18 to 0.44 grammes of solid material per kilo.

TABLE XXXVII.—*The Proportion of Bile secreted in twenty-four hours in various Animals to each Kilogramme of Body-weight and of the Weight of the Liver.*

Per 1 kilo. of body weight.	Ox.	Cat.	Dog.	Sheep.	Rabbit.	Guinea Pig.
Fresh Bile	15.0	14.50	19.99	25.41	136.84	175.84
Bile--solids	0.5	0.816	0.988	1.344	2.47	2.20
Per 1 kilo. of liver weight.						
Fresh Bile	...	...	...	1607.2	4063.2	4452.0
Bile—solids	...	...	...	99.12	91.16	64.08

The smaller the animal the larger is the ratio of bile secreted per kilogramme of its weight, and this is still more marked when the weight of the liver is similarly contrasted.

The amount of bile excreted is influenced by the quantity absorbed from the intestine. As Schiff described it, a circulation of bile occurs. The liver can make use not only of the reabsorbed biliary constituents but of biliary pigments introduced into the general blood-stream. Some animals excrete bile-pigments which are peculiar to themselves and absent in others. Baldi, making use of this fact, was able to detect the unchanged pigments of ox-bile in the bile of a dog after the injection of it into the blood-stream. Wertheimer similarly detected the presence of sheep-bile in the biliary excretion of a dog a quarter of an hour after its introduction into the circulation. A large increase in the flow of bile occurred at the same time.

When the portal circulation is arrested the supply of bile does not entirely cease, as the blood flowing through the hepatic artery allows the action of the liver to continue, although in an impaired manner. The pressure at which bile is excreted is very low when compared with that of the saliva, but is proportionately the same when the blood-pressure in the

portal vein and in the arteries supplying the salivary glands are contrasted.

TABLE XXXVIII.—*Showing the Relationship between the Pressure of the Bile excretion and that in the superior mesenteric vein in the dog.* (*Heidenhain.*)

Bile pressure.	Blood pressure.
220 mm. solution of sodium carbonate.	90 mm. solution of sodium carbonate.
175 ,, ,,	67 ,, ,,
204 ,, ,,	90 ,, ,,
110 ,, ,,	50 ,, ,,
180 ,, ,,	65 ,, ,,

The figures in the above table bear the ratio of 2.45 : 1, from which we can deduce the fact that bile is excreted at a pressure twice and a half greater than that of the blood in the superior mesenteric vein.

The Bile Acids.—A full description of the characters and properties of the various bile acids would be out of place here. The more general facts can only be noticed, while further information on the subject may be obtained from any of the text-books on physiological chemistry. The bile of all animals contains glycocholic or taurocholic acid, or both. These acids contain nitrogen; taurocholic acid contains sulphur in addition. Glycocholic acid splits up when acted on by hydrolytic agents into glycocoll (amido-acetic acid) and cholalic acid; taurocholic acid similarly yields taurin (amido-ethyl-sulphonic acid) and cholalic acid.

$$\underset{\text{Glycocholic Acid.}}{C_{26}H_{43}NO_6} + \underset{\text{Water.}}{H_2O} = \underset{\text{Cholalic Acid.}}{C_{24}H_{40}O_5} + \underset{\text{Glycocoll.}}{CH_2(NH_2)COOH}$$

$$\underset{\text{Taurocholic Acid.}}{C_{26}H_{45}NSO_7} + \underset{\text{Water.}}{H_2O} = \underset{\text{Cholalic Acid.}}{C_{24}H_{40}O_5} + \underset{\text{Taurin.}}{C_2H_7NSO_3}$$

In herbivorous animals glycocholic acid forms the principal bile acid present; in the *Carnivora* taurocholic acid is the chief, or sometimes the only, bile acid; while in man the latter is sometimes absent, and is never present in as great amount as glycocholic acid.

With the exception of fishes and certain reptiles, the bile of

animals contains sodium salts of the bile acids. Potassium takes the place of sodium in salt-water fishes, while fresh-water fishes excrete bile in which salts of the bile acids with both of these bases are found.

The Colouring Matter of the Bile.—The yellow or dull orange bile of *Carnivora*, of man, and of the pig owes its colour to the presence of a pigment, *bilirubin*. This pigment has an intense yellow colour and thus readily reveals its presence in the fæces, or, in cases of jaundice, in the blood. Solutions containing only 1 part in 500,000 are yellow when a layer of 1.5 cm. deep is looked through. When in a pure condition it may be in the form of an amorphous powder of an orange colour, or in red-orange crystals like those of chromic acid. Bilirubin has a formula corresponding to a percentage composition of (Städeler and Maly)—

Carbon - - - - -	67.13
Hydrogen - - - - -	6.29
Nitrogen - - - - -	9.79
Oxygen - - - - -	16.79

$$C_{16}H_{18}N_2O_3 \text{ or } C_{32}H_{36}N_4O_6$$

Biliverdin, $C_{32}H_{36}N_4O_8$ (Maly), is a green pigment present in the bile of *Herbivora*, and it can also be produced from bilirubin by the action of oxidising agents. When the bile of *Carnivora* is left exposed to the air it gradually acquires a green hue, due to the oxidation of bilirubin. The same change may occur in the stomach when bile has found its way into that organ. For this reason vomited matters containing bile are often of a bright green colour, and bile is consequently regarded by many as being normally of a green hue, though actually of a yellowish-brown colour.

$$\underset{\text{Bilirubin.}}{C_{32}H_{36}N_4O_6} + O_2 = \underset{\text{Biliverdin.}}{C_{32}H_{36}N_4O_8} \text{ (Maly).}$$

Hydrobilirubin is a derivative of the bilirubin of the bile through the action of reducing agents, and is formed by such agents in the intestinal canal. Of a brown or garnet-red colour in solution, it is incapable of being oxidised to biliverdin.

Urobilin, bilicyanin, and choletelin are other derivatives from the biliary pigments. The first is brownish-red in colour, the second blue, and the third yellow.

Gmelin's reaction for the presence of bile pigments—*i.e.*, the play of colours which follows the addition of nitric acid containing some nitrous acid to the solution—depends upon the production of the oxidation products of bilirubin or biliverdin. The colours pass from green to blue, violet, red to yellow, the yellow tint corresponding to choletelin, the most highly oxidised of the series.

The Nucleo-albumin of the Bile.—The mucous fluid added to the bile in the secretion of the lining cells of the gall bladder was long thought to owe its viscidity to mucin, but it has lately been shown by Landwehr that only a trace of true mucin is present, the viscidity being due to a nucleo-albumin which splits up on hydrolysis into a proteid and nuclein. This mucoid nucleo-albumin contains 16.14 per cent. of nitrogen, compared with 11 per cent. to 12.3 per cent. present in mucin.

Cholesterin, lecithin, fats, and soaps can also be separated from the bile.

The Action of the Bile.—The bile contains only an insignificant trace of a diastatic ferment, and, unlike the other glandular secretions connected with the alimentary canal, has no active ferment action. It must possess some important excretory function when we bear in mind the proportionately large quantity formed in the fœtus before any other digestive processes have commenced. Also, as Bunge argues, it is logical to assign to it some influence on intestinal digestion, seeing that it is discharged along with the pancreatic secretion high up in the bowel, and not passed out into the rectum as a waste product. Our present knowledge of its actions may be summed up as follows:—

1. Bile is able to convert very minute traces of starch into sugar (Nasse attributes a greater power of amylolysis to the bile of the pig).

2. The addition of bile to an acid solution of proteids and pepsin precipitates the native albumin, and causes a precipitation of bile acids which carries down the pepsin and renders it inert, even although the alkali in the bile is insufficient to completely neutralise the acid in the solution. The addition of the bile to the contents of the stomach when they have reached the duodenum causes such a precipitation.

3. Although digestion of carbo-hydrates and proteids proceeds normally in the absence of bile in the bowel, the

digestion of fats is greatly interfered with under such conditions.

Free fatty acids are soluble in bile, but the fat taken in with food is only partially absorbed after solution in the bile. The slightly alkaline reaction of bile is transformed into an acid reaction by the solution of fatty acids in the bowel.

Although the contents of the small intestine may possess an acid reaction owing to these fatty acids (Moore and Rockwood), and to the acids formed by bacterial growth, the coexistence of soaps is possible. Moore and Rockwood suggest that only a small quantity of alkali is required to facilitate the conveyance of part of the fat in the form of soaps to the lining epithelium, as the alkali is set free on the splitting up of the soaps, and remains in the bowel, where it can be made use of again.

Bile mixed with free fatty acids at the body temperature forms an acid emulsion which is able to hold an excess of fatty acids in solution, and to form emulsions of neutral fats by the production of soaps from the alkaline salts of the bile and the free acids. In the duodenum free fatty acids are set free by the fat-splitting ferment in the pancreatic secretion, and are available for the process. Naunyn has shown also that solutions of cholates can dissolve the very insoluble calcium and magnesium soaps which may be formed in the bowel.

4. The bile itself is fermentable. It soon decomposes on standing. When no bile flows into the intestine in man and certain animals the fæces become clay-coloured, contain as much as 11 to 13 per cent. of fat, and have an intensely fœtid odour. This odour disappears if flesh be absent from the diet. Maly and Emich and Linderberger have found that taurocholic acid is strongly antiseptic, and have suggested that the influence of the bile in inhibiting fœtid decomposition in the bowel is due to the action of this acid when set free in the duodenum. But, as Gamgee remarks, the subject is not capable of such a simple explanation, for the bile acids, as we have seen, are precipitated on admixture with the acid chyme. The only assumption which appears feasible to his mind is to suppose that the precipitation of native proteids by and along with bile acids modifies the ultimate changes which the proteids undergo when acted on by putrefactive organisms.

5. The bile is formed by the liver continuously, independently of the ingestion of food, but prolonged abstinence diminishes the amount produced. Immediately after a meal

the formation of bile increases for about an hour, then diminishes until the third or fourth hour, when the flow becomes much more abundant. Chart VII., constructed from data by Barbera, clearly shows that the nature of the food taken varies the amount of bile secreted.

The liver appears to be an organ endowed with many functions. In addition to its glycogenic action, its secretion of the bile, and to its formation of urea, it acts as a destroyer of poisonous substances absorbed from the bowel. An immense amount of work has been devoted to this subject, but it will suffice here to reproduce the following facts from a paper by Roger (*La Presse Médicale*, June 26, 1897).

The urotoxic coefficient, as defined by Bouchard, represents the number of "urotoxies"—(the amount of urine per kilogramme of body-weight required to kill an animal on injection)—eliminated in the twenty-four hours. After ligature of the portal vein, with a consequent arrest of the hepatic circulation, the number of "urotoxies" represented by the urine excreted is more than doubled.

TABLE XXXIX.

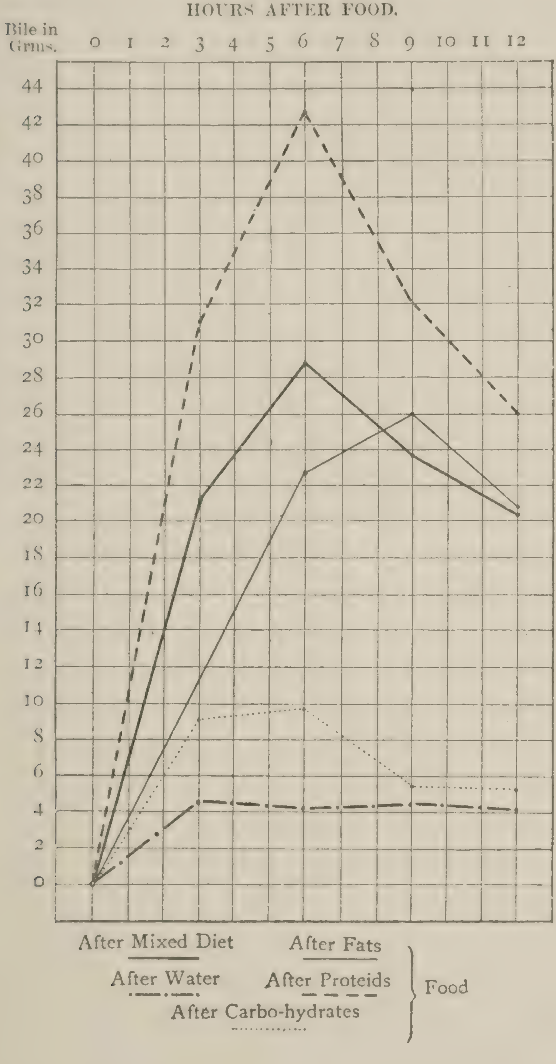
Diet.	Urotoxic coefficients. Before ligature of the portal vein.	After ligature of the portal vein.	Relation.
Flesh	0.43	0.95	1—2.2
Fat	0.34	0.87	1—2.56
Bread	0.32	0.92	1—2.87
Mixed	0.29	0.91	1—3.13
Milk	0.27	0.83	1—3.07

Milk diet, under normal circumstances, yields the smallest quantity of poisonous substances in the urine; a purely meat diet the largest. The toxicity of the urine after a mixed diet is only slightly greater than after milk alone. The proportional increase of this toxicity, after the proceeds of digestion have been prevented from passing through the liver, appears to be in reverse proportion to the original order.

Conversely, the toxicity of the bile diminishes after ligature of the portal vein. Twenty-one c. cm. of dog's bile per kilogramme of body-weight were found by Lugli to be sufficient to kill a rabbit when injected into the veins. After ligature 34 c. cm. were required. In course of time the bile secreted in animals thus treated regained a great part of its toxic properties, probably from the establishment of a vicarious supply of blood.

The liver, however, cannot be regarded as the only organ capable of shielding the organism from the toxic effects of poisons, whether of internal or external origin, as the results obtained from observations on the protective power of the suprarenal capsules, the thyroid gland, the gastric secretion, the intestinal mucous membrane, and the leucocytes of the blood, indicate the possession of similar functions, some of them perhaps more highly specialised. But the liver may be placed in the first rank of those organs which serve to defend the bodily economy from the deleterious products of its metabolism or from the harmful action of many of the poisons which may be introduced from without.

CHART VII.—Showing the quantity of Bile secreted after different forms of Food. (Constructed from data by Barbera.)



A series of observations by Pohl (*Arch. f. Exper. Path. u. Pharmak.*, xxxvii. 6, p. 413, 1896) on the fate of substances given by the mouth which are known outside the body to yield carbonic acid by their oxidation, shows that oxalic acid is not destroyed in the body; that glycolic and glycoxylic acids, which form oxalic acid when artificially oxidised, are partly decomposed without the formation of oxalic acid; that more highly oxidised acids of the same series, such as glycoxylic acid, are to be looked upon as the immediate forerunners of carbonic acid; and that malic, tartaric, and similar acids are fully burnt up in the body without increasing the output of oxalic acid.

A General Survey of the Processes of Digestion in the Small Intestine.—The chyme, which enters the duodenum from the stomach, has an acid reaction. As we have seen above, it does not enter the duodenum all at once. The benefit of a gradual emptying of the stomach into the bowel is evident, for the alkaline secretions which are poured into the upper part of the small intestine are better able to neutralise the acid of the chyme. The chyme, when it enters the duodenum, consists of water; carbo-hydrates, partly changed by the saliva, partly unchanged; proteids, many of them in simpler form than the albumins and globulins of the original food, probably a considerable portion of them unchanged; salts, and, in addition, acids, both free hydrochloric acid, hydrochloric acid combined with proteid bodies, and usually small quantities of certain organic acids. As soon as the chyme enters the duodenum a rapid absorption of water takes place. The upper part of the duodenum commences to secrete an alkaline fluid which tends in some part to neutralise its acidity. Three or four inches from the pylorus the acid chyme encounters the secretion of the pancreas and the bile. As the pancreatic juice possesses a strongly alkaline reaction, chiefly due to the presence of carbonate of sodium, it soon renders the chyme much less acid. The bile when first poured into the duodenum is neutral, but contains substances which precipitate many of the soluble constituents, such as the peptones, the albumoses and pepsin. This precipitate covers the surface of the mucous membrane in the form of a grey coating. The pepsin thus precipitated re-dissolves later, but has now been rendered inactive, and is therefore unable to destroy the pancreatic ferments, as it is able to do in an acid medium. Although it has been stated in numerous text-books and by numerous authorities that the contents of the small intestine are rapidly rendered alkaline by the secretions of the pancreatic and intestinal glands, it is a

fact that in the dog and in man they seldom become alkaline in any part of it. (Chart VI.)

The earlier statements as to the contents being alkaline were based solely on the reaction of the various intestinal juices, and not upon practical examination of the contents themselves. The reason that the reaction remains acid is to be ascribed to the presence of acid-forming micro-organisms. One of the functions of the free hydrochloric acid in the stomach is to destroy or inhibit the bacteria taken in with the food. The secretion is antiseptic. Many of the organisms, however, are only inhibited, their growth is delayed, not destroyed, and whenever the contents are rendered less acid they are again enabled to grow. In addition, the small intestine is not divided from the large by any structure which can prevent organisms indigenous to the large intestine from reaching the contents of the small. In health the organisms which flourish in the small intestine are mainly those which produce acids by their fermentative action. The chief acids formed by them are acetic acid and lactic acid. The moment the chyme has been sufficiently neutralised by the alkaline secretions of the intestinal glands, the bacteria present are able to flourish in it. In fact, there is a kind of paradox involved. The more alkali secreted by the intestinal glands the better the organisms are able to flourish and the greater is the amount of acid produced by them.

The acid chyme, then, is rapidly made less acid by the alkali poured into the duodenum, the free hydrochloric acid present in it combines with the sodium of the sodium carbonate forming chloride of sodium, the hydrochloric acid combined with the proteid bodies is then acted on, while much of the proteid material in it is precipitated by the action of the bile. Still the organic acids produced by the action of micro-organisms prevent the contents from becoming actually alkaline.

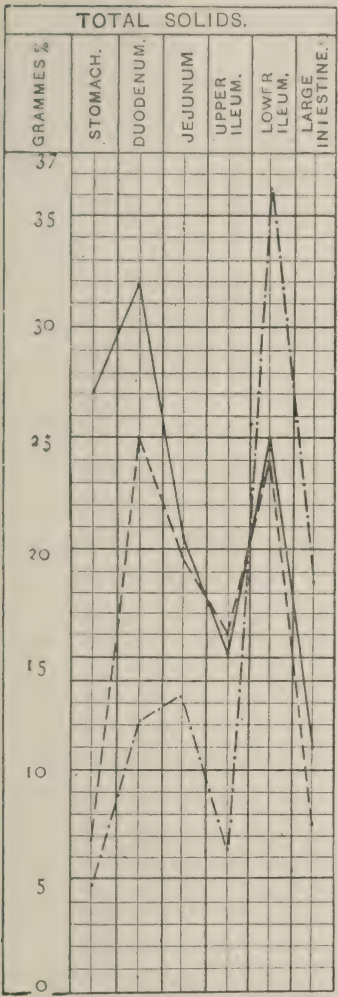
In the secretion of the pancreas four ferments are added to the contents. A proteolytic ferment, trypsin, a diastatic ferment, called amylopsin, which can convert starch into sugar, and a ferment which acts upon fats, splitting up neutral fats into glycerine and fatty acids. Another ferment has been described, a pancreatic milk-curdling ferment. The admixture of bile to the pancreatic secretion enables emulsion of fats to take place more readily, while the salts of the bile acids split

up in a short time into salts of other bases and into bile acids. These bile acids exert an antiseptic action on the intestinal contents (cf. p. 193). The diastatic ferment of the pancreatic juice acts in a similar way to that of the saliva, the process of conversion of starch going no further than the production of dextrins and maltose, or malt sugar. The secreting glands which stud the walls of the small intestine pour out a juice with a slightly alkaline reaction, containing a ferment which is capable of finishing the work done by the saliva and the pancreatic secretion in the conversion of starch into sugar by inverting maltose into dextrose and lævulose. The changes in the contents thus described take place as they proceed down the tube. The contents do not become more concentrated than in the duodenum, but rather less so, as the fluid secreted by the different glands more than compensates for the amount absorbed by the intestinal walls, while a considerable proportion of the solid matters is absorbed during the downward course. (Chart VIII.) Trypsin acts energetically on the proteids which have passed through the stomach in an undigested form. Starch, cane-sugar, and maltose are converted into glucose, and the fats split up or emulsified.

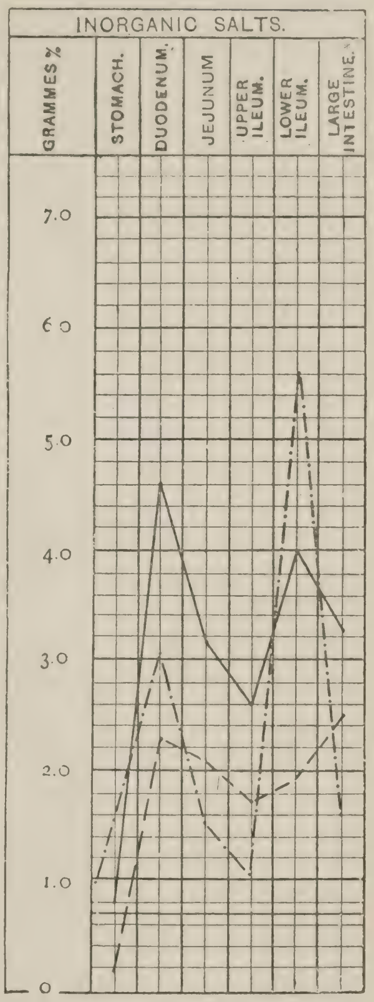
The great function, therefore, of the small intestine is not the absorption of fluid so much as the absorption of soluble solids. There is no doubt that rapid absorption may take place in the duodenum, but below this the contents of the bowel become rather more fluid. In the normal state, although large numbers of bacteria flourish in the intestinal contents, a great majority of them are those which produce organic acids by their fermentative action. The acids formed by them arrest the growth of the bacteria which bring about true putrefactive changes. These putrefactive bacteria are very sensitive to the action of acids, as may be easily understood when it is mentioned that most of them render the medium in which they grow alkaline in reaction. The preponderance of the acid-forming organisms in the intestine, perhaps, may be explained by the fact that they are less easily destroyed by the acid of the stomach, and are, therefore, more likely to pass through that organ unscathed.

Digestion in the Large Intestine.—The contents of the lower part of ileum when they pass through the *ileo-cæcal* valve are more or less fluid, yellow or light brown in colour, and possess a sour but no putrefactive odour. The flow appears to be

A



B



DOG { (UNFILTERED.)
(FILTERED.)
CALF— (UNFILTERED.)
AVERAGE PROPORTION OF SOLIDS AND ASH IN MILK

A. To show the Total Solids per cent. in the Contents of the different divisions of the Alimentary Canal in the Dog and Calf fed on Milk alone.

B. To show the Inorganic Salts in the same.

* The Large Intestine in the Dog had been emptied shortly before Death.

constant, but to be less during the night than in the day-time. Macfadyen, Nencki, and Sieber found that the time elapsing between the ingestion of food and its appearance at the *ileo-cæcal* valve varied greatly in the same person. Thus in the case of a patient with a fistulous opening at the junction of the ileum and the colon, from $2\frac{1}{4}$ hours up to $5\frac{1}{4}$ hours elapsed between the swallowing of green peas and their first appearance at the opening, while from 14 to as many as 23 hours passed before the last of the peas were discharged on the different occasions on which the experiment was performed.

The contents as they enter the colon are generally of an acid reaction, and contain albumin, mucin, a small proportion of the derivatives of proteid digestion, and of the conversion of starch, along with lactic and volatile fatty acids, bile acids, and bilirubin.

Macfadyen, Nencki, and Sieber found in a man on a mixed diet that the total solids of the contents passing through the lower end of the ileum amounted only to 5 per cent.; when food yielding a more solid residue was given, the solids rose to about 10 per cent. On one occasion 26.95 grammes, and on another 26.05 grammes of solid matter were passed in 24 hours. In a dog fed on sterilised milk the writer obtained much higher figures from the estimation of the solids in the lower part of the ileum—viz., 25 per cent., and in a sucking calf as much as 32 per cent. The constituents of the solid matter entering the large intestine comprise about 30 to 42 per cent. of proteid bodies, 8.5 per cent. of fats, 45 per cent. of carbo-hydrates and other alcoholic extractives, and about 8.5 per cent. of inorganic salts. These proportions are subject to very considerable variations. In health neither indol, leucin, nor tyrosin are present. (Chart VIII.)

In the small intestine the action of micro-organisms on the contents is confined almost exclusively to the carbo-hydrate moiety present. In the large intestine putrefaction of albuminous substances may occur. (Cf. p. 219.)

The secretion of the glands of the large intestine is strongly alkaline, even more so than the succus entericus of the small bowel. The contents, however, remain acid in reaction owing to the products of bacterial activity. The continued growth of bacteria is possible, notwithstanding the presence of acids formed by them, by reason of the constant addition of alkali by the glands of the mucous membrane. But for this

the acidity would soon rise above a point inimical to bacterial life.

The secretion of the large intestine contains neither a proteolytic nor a diastatic ferment. Any digestive change which can occur in its contents must proceed from the presence of ferments added above, or, and this more especially, from the action of micro-organisms. The mucous membrane, however, is capable of absorbing soluble albumins, peptones and albumoses, sugars and water. This property is made use of in the rectal alimentation of patients. Uncoagulated albumins in solution do not appear to be absorbed except in the presence of a neutral salt.

Although the secretion of the large intestine is devoid of ferments, and in the *carnivora* and man the processes carried on in that part of the bowel are chiefly absorptive, in the *herbivora*, other than ruminants, the large intestine, especially the *cæcum*, is of great size, and acts as a receptacle for partially digested food, where it undergoes the same fermentative change as in the rumen of the *ruminantia*, where cellulose is digested through the agency of bacteria.

In the animal kingdom, the development of the large intestine, and the importance of the processes carried on in it (and this applies more particularly to the cæcum), vary inversely to the size of the stomach or the completeness of gastric digestion. The stomach of the horse is small, and only partially able to cope with the material given it; of the cow, large, and capable of very thorough digestion of the food; and of the dog, of moderate size, but endowed with active properties and aided by vigorous digestive processes in the small intestine: so in the horse the large intestine is enormously developed, in the cow much less so, while in the dog it is small and short.

The Fæces.—The characters and composition of the fæces vary with the amount and nature of the food taken, and especially with the proportion of indigestible matter consumed. In *carnivora* the small residue left after the digestion of meat causes the fæces to be scanty and firm. For the same reason a milk diet leads to dry and small evacuations. In *herbivora* the ingestion of large amounts of food with a low nutritive value, and containing much indigestible matter, accounts for the copious evacuations of these animals. In them, too, the amount passed is proportionately greater when compared with the food taken, owing to an increased percentage of water dis-

TABLE XL.—*Percentage of Food-Stuffs passed in the Fæces.*

Animal Foods.	Roast Beef of 1435 grm.	Roast Beef of 1172 grm.	Milk of 2050 grm.	Milk of 2433 grm.	Milk of 3075 grm.	Milk of 4100 grm.	Milk and Cheese. 200 grm. Cheese. 2291 grm. Milk.	Milk and Cheese. 218 grm. Cheese. 2050 grm. Milk.	Milk and Cheese. 517 grm. Cheese. 2209 grm. Milk.	Hard-boiled Eggs. 20 Eggs = 948 grm.	Bacon. 99 grm.	Bacon. 195 grm.	Butter. 214 grm.
	%	%	%	%	%	%	%	%	%	%	%	%	%
Dried Total Solids ..	4.7	5.6	8.4	7.8	10.2	9.4	6.0	6.8	11 3	5.2	—	—	—
Nitrogen	2 5	2.8	7.0	6.5	7.7	12.0	3.7	2.9	4.9	2.9	—	—	—
Fat	21.1	17.2	7.1	3.3	5.6	4.6	2.7	7.7	11.5	5.0	17.4	7.9	2.7
Ash	15.0	21.2	46.8	48.8	48.2	44.5	26.1	30.7	55.7	18.4	—	—	—
Organic Substances..	—	—	5.4	—	—	—	4.6	—	—	—	—	—	—

Vegetable Foods.	Morning Rolls. 439 grm. Dried.	Bread. 455 grm. Dried.	Bread. 779 grm. Dried.	Rice. 660 grm. Dried.	Peasoup. 521 grm. Dried.	Peasoup. 960 grm. Dried.	Potatoes. 3078 grm. Undried. 819 grm. Dried.
Dried Total Solids	5 6	5.2	3.7	4.1	9.1	14.5	9.4
Nitrogen	19.9	25.7	18.7	20.4	17.5	27.8	32.2
Carbo-hydrates	—	1.4	0.8	0.9	3.6	7.0	7.6
Ash	30.2	25.4	17.3	15.0	32.5	38.9	—

charged along with it. The horse empties his bowel once in about every three hours, and on an ordinary diet will pass in the day about 17 kilogrammes of fæces containing 2.6 kilogrammes of solids. Thirty kilogrammes of fæces with 4.6 kilogrammes of solid matter forms a fair average in cows, while dogs on a purely meat diet may only discharge a few grammes every second day. In man one-seventh to one-eighth of the solid food taken in is evacuated from the bowel, or about 150 grammes *per diem*. The more rapid the course of the food through the bowel, the greater is the proportion discharged. (Table XL.)

A comparison between the average composition of the contents of the ileum as they pass into the colon, and that of the fæces in man, will serve to illustrate the changes which take place during their progress through the large bowel.

TABLE XLI.—*Composition of the Contents entering and leaving the Large Intestine.*

	Water.	Total Solids.	Organic Solids.	Salts.
Contents at ileo-cæcal valve ...	90-95 % ...	5-10 % ...	4.58-9.15 % ...	0.42-0.85 %
Fæces	68.7-82.6 % ...	17.4-31.7 % ...	10.7-25.0 % ...	6.7 %

SOLIDS.

	Proteids and Mucin.	Fats.	Carbo-hydrates and Extractives.	Salts.
Contents at ileo-cæcal valve ...	30-42 % ...	8.5 % ...	45 % ...	8.5 %
Fæces	0-;0 % ...	11.5-15 % ...	15.6-22 % ...	24.2-38.5 %

Defæcation.—Defæcation is partly a voluntary and partly a reflex act. The contents of the intestine are constantly propelled in a direction from the mouth towards the anus by the peristaltic or worm-like movements of the walls. At the lower extremity of the gut their progress is arrested by the resistance offered by the anal sphincter or muscular ring, which normally remains contracted and closed. The sphincter is formed of two layers, an internal composed of involuntary fibres, and an external of voluntary muscle fibres. A nerve-centre in the lower or lumbar part of the spinal cord, by a constant passage of nerve impulses, maintains the contraction of these muscles. When fæces enter the rectum, their presence causes a desire

to defæcate, and leads to the arrest of the nerve impulses to the sphincter muscles, both reflexly from the rectum and voluntarily from the brain. When the muscular rings are relaxed the peristaltic movements of the rectal walls alone are sufficient to evacuate the contents, but they are usually aided by voluntary contractions of the muscles in the abdominal wall.

CHAPTER IX.

ABSORPTION FROM THE ALIMENTARY CANAL.

Heidenhain's laws — Proteids — Sugars — Salts — Fat — Osmosis — Vital action—Change in form of absorbed proteids—Course of absorbed material—Lymph duct—Chyle.

The Process of Absorption in the Alimentary Canal.—At one time it was generally supposed that absorption of the products of digestion, and of the fluids taken with the food, was simply the outcome of a simple act of diffusion, as first described by Graham. The researches of Cahn and von Mering, and of others, upon absorption in the stomach show clearly that the laws of osmosis cannot apply to the process of absorption of digestive products in that organ. Little or no water is absorbed by the mucous membrane of the stomach, while sugar, salts, and peptones can be taken up. The rate of absorption from the stomach has been found to be increased when such substances are given dissolved in alcohol, while alcohol itself rapidly passes through the gastric mucous membrane into the blood-stream. These observations are sufficient to negative the supposition that simple diffusion plays the greater part in the absorption of fluids, or of the bodies which they contain in solution. Heidenhain (*Pflüger's Archiv.*, lvi. s. 579) placed the laws of absorption in the alimentary tract on a securer basis. The chief laws of diffusion are as follows :—

1. Watery fluids of equal osmotic value on either side of a dialysing membrane retain the same volume.
2. Fluids of unequal osmotic value alter in volume; some of the water of the fluid with the lesser passing through the membrane to the side of the fluid with the greater value until the value becomes equalised.

3. The osmotic value of each solution is equal to the sum of its single constituents.
4. If the total osmotic value in a mixed solution be equal, but that of the single constituents different, and portions be placed on either side of a dialysing membrane, the individual constituents become equalised, although the volume remains the same. If absorption in the alimentary canal were the result of simple diffusion, it would necessarily follow these conditions. In such a case, fluids corresponding in osmotic value to blood, or with a value which is smaller, could not be absorbed.

Heidenhain found that blood-serum placed in the intestine of a dog was absorbed by the mucous membrane, although by the addition of intestinal secretion its osmotic equivalent had been rendered less than that of the blood circulating in the walls. Again, dog's blood-serum placed in the intestine lost water and salts in a ratio corresponding to their original proportions, while the organic substances diminished in much smaller proportion. Using solutions of common salt, he found that whether the osmotic equivalent was above or below that of the blood, interchange took place. When, therefore, the osmotic equivalent of a salt solution is higher than that of the blood and absorption occurs, the cells lining the mucous membrane must have some action in the process. On the other hand, as water and the salt dissolved in it are absorbed in proportion to the amounts present, osmotic force must also have some influence.

As the proportion of salt increases in the contents of the bowel, the absorption of fluid becomes larger, and as the osmotic force of the fluid is increased by the greater percentage of salts contained in it, the salts are also absorbed in greater quantity. If the laws of simple diffusion were followed, water would flow from the blood into the contents; but this does not occur, owing to an inhibitory power, placed by Heidenhain in the epithelial cells lining the mucous membrane. The greater the proportion of salts in the contents the greater is the opposition exercised by the cells to the flow of water from the blood. In certain concentrations the absorption of water ceases, while salts are still removed. With 2 per cent. of common salt the absorption of salt stops, while with 0.3 to 0.5 per cent. of salt the process proceeds both by the absorption due to osmotic force and by physiological action. If fluoride of sodium in small quantities be added to a chloride of sodium solution introduced into the bowel, the physiological path of absorption is blocked, while the water absorption from the salt

solution is increased. Thus when the strength of the fluoride of sodium solution be above 0.04 to 0.05 per cent., the epithelium of the gut is altered, water absorption is increased, and removal of salt lessened.

Other circumstances point to the fact that absorption from the alimentary tract cannot solely be due to simple diffusion. For instance, cane-sugar, which is highly diffusible through dead animal membranes, is scarcely taken up at all from the bowel. Grape-sugar, which is not nearly so diffusible as sodium sulphate, is absorbed from a loop of intestine much more rapidly than that salt. Albumin, again, which does not pass through dead animal membranes, is, to a certain extent, absorbed by the mucous membrane of the living bowel without change. Thus, Friedländer (*Zeitschrift für Biologie*, xxxiii. 2) found that both egg and serum albumin were absorbed up to a proportion of 20 per cent. in an isolated loop of the small intestine, while 60 per cent. of alkali-albumin, 90 per cent. of commercial peptone, and 70 per cent. of albumoses were similarly absorbed. The albumin seemed to be absorbed as such, not in the form of any of its derivatives. Neither casein, acid-albumin, nor myosin were absorbed to any appreciable extent, although the acid used to dissolve them was rapidly removed.

The absorption of fats is carried out by the epithelial cells of the villi in the upper part of the small intestine. They are not absorbed in solution but in a state of fine division, and, to some extent, in the form of soaps. If an animal be killed during digestion of a fatty meal the epithelial cells in the villi may be seen to contain globules of different sizes which stain black with osmotic acid, are dissolved by ether, and which are therefore fatty. We do not know how the cells take up the fat particles from the bowel contents, but they certainly pass through and not between the cells. The particles have, indeed, been described as pushing their way between the cells and then being taken up by wandering white blood corpuscles or leucocytes. But, in the first place, the fatty granules discovered between the cells had, in all probability, been forced between them by shrinkage of the tissue during its histological preparation. In the second, the granules looked upon as fat in white blood corpuscles or leucocytes are not soluble in ether, as true fat is.

A dog normally absorbs 9 to 21 per cent. of the fat swallowed with food in three to four hours, from 31 to 46 per cent. in seven hours, and 86 per cent. in eighteen hours (Harley). After extirpation of the pancreas the small intestine has been found four to seven hours after a meal to contain more fat than was taken in with the food. This seeming

impossibility is explained by the fact that excision of the pancreas partly prevents the absorption of the fats present, while the mucous membrane of the intestine normally excretes fats into the bowel. The extirpation of the pancreas does not entirely prevent the absorption of fatty particles, because the lacteal vessels running from the bowel are filled with a milky chyle, but the amount absorbed is less than the amount re-excreted into the bowel.

Proteids are absorbed for the greater part after their alteration into simpler derivatives, although there is no doubt that native albumins and globulins may be absorbed as such. The physiological factor has much to do with the absorption of proteid bodies, more than with the absorption of salts or of water. The epithelial cells lining the villi are the chief agents in the process, and they probably have a second function in addition to that of absorption. That is to say, the proteid derivatives absorbed from the contents of the bowel by the one side of the cells, reach the blood-stream on the other side of the cells in the form of native albumins and globulins again.[1] How this change is brought about is unknown.

There may be some connection between the amount of carbonic acid in blood and the alteration of the proteids absorbed by the stomach and bowel. Lahoussen found that if he injected 0.3 gramme of peptone per kilogramme of the body-weight into the blood-stream of a dog, the amount of carbonic acid in the blood sank to a half; 0.5 gramme per kilo. caused a decrease of one quarter. The loss in the amount of carbonic acid lasted from one to two hours. There was no diminution in the temperature of the animal.

The peptones and albumoses absorbed by the mucous membrane of the alimentary tract may in this way cause a diminution in the amount of carbonic acid in the blood, or blood-serum, circulating through it. May it not be possible that the anabolic metamorphosis of peptone and albumoses resulting in the re-formation of albumins and globulins is due to gaseous substances present in the blood, interchanging with gaseous elements in the lumen of the tract?

The constant presence of carbonic acid gas in the stomach (Schierbeck, *Skandin. Arch. f. Physiol.*, 1891, Bd. iii. s. 437) is of importance with regard to this question. In the empty stomach this gas is present at a pressure of from 30 to 40 mm. of mercury. During the height of digestion the pressure rises to 130 or 140 mm. If the stomach be thoroughly washed

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[1] Waymouth Reid introduced into an isolated loop of the intestine of a goose 50 c. cm. of a 1 per cent. solution of albumoses and peptones, free from albumins and extractives, made from Grübler's commercial peptones by precipitation with trichloracetic acid. 48 c. cm. were recovered after three minutes, containing 98.41 per cent. of the proteids introduced.

out and all the carbonic acid removed, in a short time it is again secreted, until the pressure once more equals 30 to 40 mm. Part of the gas may be the result of an interchange between the oxygen of the air swallowed and the carbonic acid in the blood. As, however, carbonic acid gas passes into the stomach after the organ has been emptied, reaching to what we may assume to be its normal pressure, while this pressure increases enormously during active digestion, simple interchange with the oxygen of any air which has been swallowed is insufficient to account for its presence in such quantities. Some function, as yet undiscovered, probably pertains to the changes of pressure of carbonic acid in the blood and within the alimentary tract during digestion, and may have to do with the proteid metamorphosis in the intestinal walls.

The Course of the Absorbed Materials.—The water, salts, and sugar absorbed through the alimentary canal pass normally into the smaller branches of the portal veins, and by them are conveyed to the liver. There is no increase in the quantity of those substances in the chyle during digestion, while sugar increases in quantity in the portal blood. In man about 1 per cent. of the sugar, corresponding to 1 per cent. of the carbo-hydrates in the food, may be discovered in the contents of the lymphatic duct. (See Table XLII.)

Chyle.—Fats chiefly enter the small terminal branches of the lymph vessels which pass into each villus of the intestinal mucous membrane and are thence carried to the chief lymphatic vessel in the body, the thoracic duct. The junction of the numberless small lacteal vessels into intermediate larger ducts, and finally of these into the thoracic duct, provides a channel by which fats and any of the other products of digestion which have not entered the blood-stream of the portal system can be added to the circulating blood at a spot where their transit through the liver before arrival at the heart is avoided. Veins of the neck fulfil this condition, and it is into them that the duct empties. When a meal rich in fat has been given to an animal shortly before death, on opening the abdomen numbers of bright glistening lines can be seen running from the upper part of the small intestine across the mesentery which attaches the bowel to the posterior wall of the abdomen. These are the lymph vessels filled with chyle, and owing their white colour to the presence of fats in a state of very minute sub-division within their walls. The fats of the food which have been saponified by the action of the alkalies in the intestinal secretions are absorbed by the veins and carried to the liver, but at least two-thirds of the fat given enters the

TABLE XLII.—*Analyses of Lymph and Chyle in Man and various Animals, in parts per* 1000.

	I.—In Man.								II.—Of the Horse.			III.—Of the Dog.	
	Lymph.					Chyle.			Chyle.		Blood-Serum.	Chyle.	Blood-Serum.
	1.*	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
Water	939.9	934.8	969.3	957.6	986.3	943.6	904.80	943-958	960.97	956.19	930.75	906.77	936.01
Solids	60.1	65.2	30.7	42.4	13.7	56.4	95.20	41-56	39.03	43.81	69.25	96.23	63.99
Fibrin	0.5	0.6	5.2	0.4	1.1	1.6	70.80	11-13	2.57	1.27	—	1.11	—
Albumin	42.7	42.8	4.3	34.7	2.3	21.2			22.60	29.85	56.59	21.05	45.24
Fats	3.8	9.2	2.6	—	1.5	24.8	9.2	25-27	0.85	0.81	1.57 (Soaps)	64.86	6.81
Extractives	5.7	4.4	3.1	—		1.6	10.8		5.37	2.24	3.85	2.34	2.91
Salts	7.3	8.2	15.4	7.3	8.8	7.2	4.4	6.25	7.59	7.49	7.14	7.92	8.76

* 1 and 2 by Gubler and Quevenne, 3 by Marchand and Colberg, 4 by Scherer, 5 by Dähnhardt and Hansen, 6 by Odenius and Lang, 7, 9 to 13 from Hoppe-Seyler, 8 by Noël Paton.

TABLE XLIII.—*Composition of the Chyle in the Thoracic Duct, in parts per* 1000.

	Man.			Dog.	Horse.	
	1. (Hoppe-Seyler.)	2. (Gubler.)	3. (Lymph.) (Marchand.)	(Hoppe-Seyler.)	(Hoppe-Seyler.)	
Water	940.224	939.9	969.3	906.77	960.97	956.19
Total Solids	59.276	60.1	30.7	96.23	39.03	43.81
Proteids	36.665	43.2	9.5	22.16	25.17	31.12
Fibrin and Globulin	6.925	0.5	5.2	1.11	2.57	1.27
Albumin	29.740	42.7	4.3	21.05	22.60	29.85
Fats, etc.	9.376	3.8	2.6	64.86	0.09	0.53
Fat	7.226					
Lecithin	1.321					
Cholesterin	0.829					
Extractives	4 208	5.7	3.1	2.34	5.42	2.30
Soaps	2 355	—	—	—	0.76	0.28
Total Organic Solids	52.122	52.8	15.3	88.31	31.44	36.32
Ash	7.154	7.3	15.4	7.92	7.59	7.49
NaCl					5.76	5.84
NaHO					1.13	1.17
KHO						0 13
SO_3					0.07	0.05
P_2O_3					0.01	0.05
$Ca_3(PO_4)_2$, $Mg_3(PO_4)_2$					0.44	0.25
CO_2					1.02	0.82

chyle duct in a fine emulsion and is conveyed by it to the venous vessels at the root of the neck.

TABLE XLIV.—*Average Composition of Chyle and Lymph.*

(In parts per 1000.)

	Man. Chyle. 1. (Paton.)	Man. Chyle. 2. (Reis.)	Man. Lymph. 1. (Munk.)	Man. Lymph. 2. (Mean of 6.)	Horse. Chyle. (Hoppe-Seyler.)	Horse. Chyle. (Hoppe-Seyler.)	Horse. Lymph. (Mean.)
Water	953.4	904.8	950.0	955.25	960.97	956.19	959.65
Total Solids ..	46.6	95.2	50.0	44.75	39.03	43.81	40.35
Organic Solids ..	40.1	90.8	45.0	35.72	31.44	36.32	33.01
Inorganic Salts ..	6.5	4.4	5.0	9.03	7.59	7.49	7.34
Proteids ..	13.7	70.8	41.0	26.21	25.17	31.12	28.76
Fats	24.06						
Lecithin ..	0.6	9.2	Trace	6.90 (?)	0.85	0.81	1.17
Cholesterin ..	0.36						
Extractives ..	1.38	10.0	3.0	2.61	5.42	4.39	3.08

The Values are deduced from the figures given in the preceding Tables.

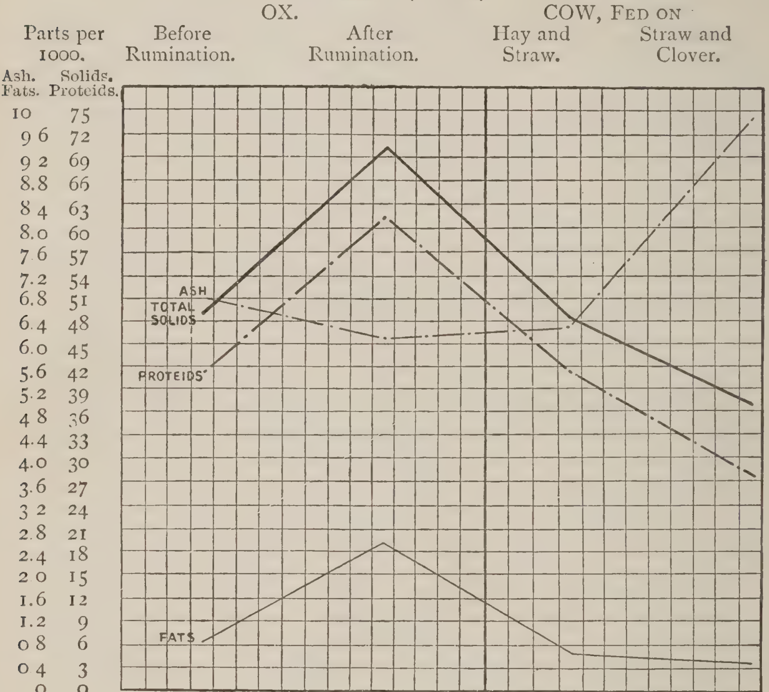
In *Herbivora* the chyle in the thoracic duct is slightly opalescent, or even transparent and of a yellow colour. In *Carnivora*, *Omnivora*, and suckling *Herbivora* it is milky in appearance.

The figures given in Tables XLII.-XLIV. show that the proportion of fat in the general blood-stream is very much below the percentage of fat present in the contents of the thoracic duct. The normal proportion in the blood remains unaltered even after the ingestion of a meal rich in fats, although fats are being added to the venous blood in considerable excess. It follows, therefore, that fats are converted into other substances in the blood. Cohnstein and Michaelis (*Pflüger's Arch.*, lxv. s. 473) could detect no increase in the proportion of fat in the blood after direct injection of chyle-fat into the vessels, nor any sign of fat excretion in the urine, or transudation into the lymph. They mixed blood with chyle out of the body, and found a disappearance of 50 per cent. or more of the original fat when air was passed through the mixture for sixteen to twenty-four hours. No diminution of fat could be detected if a current of air was not conducted through the blood and chyle, or if blood-serum alone was used. (Chart IX.)

The lipolytic or fat-destroying property of the blood cannot be exerted upon milk or liver fats.

The product of the reaction is a solid not a gaseous body, taking up carbonic acid from the air conducted through the

CHART IX.—Showing the Changes in the Composition of Chyle in Ruminants (Würtz).



mixture, or from the gas contained in the blood. It may be of the nature of a soap, but substances which are easily saponified, such as the ester of phenol-benzoic acid, are not affected by the action.[1]

[1] Harriot (*Bullet. Acad. de Méd.*, November 10, 1896) states, however, that a soluble saponifying ferment can be isolated from the blood-serum capable of acting on emulsified fats, apparently from any source, and of doubling the amount of fatty acids and glycerine. The presence of this "*lipase*," analogous to the *steapsin* of the pancreatic secretion, explains the mechanism of the intimate nutrition (so Harriot) of the tissues by fatty substances, as its action proceeds until the fatty acids become more and more simple in character—*i.e.*, butyric, acetic, and carbonic acid, until finally the salts formed by them become double compounds, leaving carbonates and giving off carbonic acid.

CHAPTER X.

THE MICRO-ORGANISMS OF THE ALIMENTARY TRACT OF THE HIGHER MAMMALS.

Micro-organisms in the Mouth—Stomach—Intestines—Chemical Poisons formed by them--Cadaveric Alkaloids—Ptomaines—Leucomaines.

LARGE numbers of bacteria flourish in the mouths of all animals. It would not be worth while to enumerate here all the different varieties which have been grown from the secretions and accretions thus found in the mouth. The organisms chiefly flourish round the bases of the teeth, and form a large part of the tartar so common in that locality. The food, when uncooked, contains in the great majority of cases a large number of micro-organisms. If fresh food be eaten hot, after thorough cooking, very few bacteria are swallowed. Raw food, especially the green food of the *Herbivora*, permits of large numbers of bacteria finding their way into the alimentary tract. In man also, meat which has been too long kept, and foods which have been insufficiently preserved, contain large numbers of these fungi which are thus introduced into the body.

When the organisms swallowed with the food reach the stomach in the *Carnivora* or *Omnivora*, they can grow unchecked or only slightly checked during the first quarter- or half-hour. In the *Herbivora*, such as the horse, the growth persists throughout a considerable period of the time during which the food stays in the stomach, while in the *Ruminantia* a large part of the digestion of cellulose proceeds in the rumen through fermentative processes due to bacteria; some say as much as 60 to 70 per cent. is thus digested. In the *Carnivora* the

inhibitory action of the hydrochloric acid secreted by the gastric cells begins to act about half-an-hour to three-quarters of an hour after the food is taken, varying, as we have seen, with the quantity of proteid contained in the food, and, therefore, with the time at which the free hydrochloric acid appears in the contents. In the *Herbivora*, the action of the hydrochloric acid on the bacteria begins when the food enters the fourth part of the stomach. The acidity of the contents proceeding from hydrochloric acid reaches, as a rule, 0.3 to 0.4 per cent. before the end of digestion. Early observers, finding that 0.3 to 0.4 per cent. of free hydrochloric acid destroyed most bacteria, argued that one of the chief actions of the gastric juice was an antiseptic one. The discovery, however, that when the hydrochloric acid after secretion combines with the proteids of the food taken, and is then much less antiseptic in its powers, has altered this conception of the bactericidal action of the gastric juice. The amount of free hydrochloric acid present rarely exceeds 0.1 to 0.15 per cent. Few of the organisms, except those very susceptible to the action of acids, are killed. On the other hand, the presence of this amount of free acid inhibits their active growth in the stomach.

MacFadyen has proved by direct experiment that the Staphylococcus pyogenes aureus and the Micrococcus tetragenus can pass through the healthy stomach without harm, while the spores of other bacteria are seldom affected. Capitan and Moreau found in a bacteriological investigation of the stomach contents of thirty individuals only three kinds of micro-organisms, two of these being moulds and one a bacillus. Abelous found sixteen different forms in the stomach-washing in his own case. Seven of these were identified, viz.—Sarcina ventriculi, Bacillus pyocyaneus, Bacterium lactis ærogenes, Bacillus subtilis, Bacillus mycoides, Bacillus amylobacter, Vibrio rugula, while of the remaining nine, eight were bacilli and one a coccus. Most of these organisms were found to be able to withstand the action of .17 per cent. hydrochloric acid for a long time, especially if they contained spores. Four of these organisms peptonised the casein of milk without coagulating it. Milk was coagulated by thirteen of the number, nine of these dissolving up the coagulum on further growth. All the organisms obtained acted more or less upon carbo-hydrates. The author, in an investigation into the bacteria present in the stomach in man (*Journal of Pathology and Bacteriology*, February 1893), was able to isolate twenty-four separate organisms, many of which were able to grow in a high percentage of hydrochloric acid, if most of it, however, was combined with proteids. Rummo and Ferranini have found that 0.05 per cent. of hydrochloric acid delays the alcoholic, the lactic, and the butyric acid fermentations, while 0.1 to 0.2 per cent. of the free acid—the normal amount of free acid generally present—stops these fermentations entirely.

Hirschfeld observed that 0.07 to 0.08 per cent. of hydrochloric acid is sufficient to arrest the action of the Bacillus acidi lactici on milk.

In the *Herbivora*, and especially in *Ruminantia*, the organisms which flourish during the early stages of gastric digestion are almost entirely those which cause acid fermentation of the carbo-hydrates of the food.

The lactic acid fermentation, which occurs in the stomach during the earlier part of digestion, is mainly the result of the growth of Bacillus acidi lactici. This organism appears under the microscope as a thick bacillus .1 to 1.7μ[1] long and .3 to .4μ broad. It often occurs in pairs, and forms spores in milk. It grows in solutions of milk-sugar, cane-sugar, and dextrin, forming lactic acid and carbonic acid.

Hüppe states that when about 0.8 per cent. of lactic acid has been formed the action of this organism ceases, but can commence again on the solution being neutralised. Starch is first converted by it into sugar, from which the acid is afterwards formed. Another organism which acts in much the same way upon carbo-hydrates is the Bacterium lactis ærogenes of Escherich.

Butyric acid is formed by many bacteria from carbo-hydrates. The organism which probably evolves the butyric acid found sometimes in the gastric contents during the first stage of the digestion of milk is the Bacillus butyricus. This organism is also able to decompose cellulose with the formation of marsh gas, carbonic acid, and sulphuretted hydrogen, and to change the lactic acid formed by the bacilli mentioned above into butyric acid.

Other organisms, especially the yeasts and the moulds, can form acetic acid, alcohol, and other products from the carbohydrates of the foods.

A peculiar organism often met with in the stomach-contents of both man and animals may be mentioned here. This is the Sarcina ventriculi, first described by Goodsir in 1842. It grows in groups of eight, arranged in a characteristic manner like that of bales of wool—in fact, the groups are known by the name of "wool-packs." Little is known about the exact rôle which this organism plays in the fermentative processes in the stomach. It undoubtedly produces an acid during its growth, and is capable of living in a solution of a very considerable acidity. The author has obtained Sarcinæ in a living condition from stomach contents with an acidity as high as .48 per cent. One or two other Sarcinæ occur,

[1] μ = micro-millimetre, $\frac{1}{1000}$th part of a millimetre, or 0.000039 inch.

but these are only occasional forms derived from the air. They are of much smaller size than the Sarcina ventriculi.

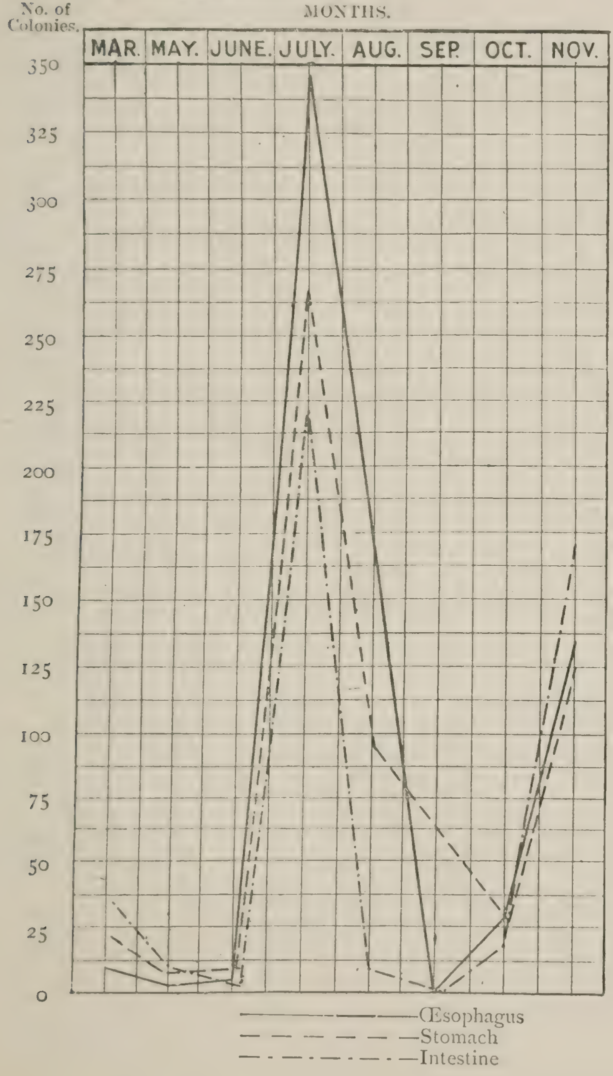
To summarise: the growth of micro-organisms in the stomach of animals and man is checked by the gastric juice during the later processes of normal digestion, but the forms which are able to produce organic acids by their growth, manufacture more or less of this acid during the earlier parts of the digestive process. The acids thus formed are chiefly lactic and butyric acids. In addition, carbonic acid and hydrogen gases may be produced by their action.

The Bacteria of the Small Intestine.—Those micro-organisms which have not been killed by the acid of the stomach juice soon grow again when they reach the small intestine; and, as the acid-forming organisms are those which can the more readily and with the least harm withstand the action of the acid in the stomach, it is those forms chiefly which flourish in this part of the alimentary canal.

In addition to these organisms, however, many putrefactive bacteria or bacilli may be present. They, however, do not flourish in the small intestine unless the acid-forming organisms have been overpowered by their numbers, or by some abnormal condition of digestion. (Cf. Charts VI. and X.)

Nencki, Macfadyen, and Sieber identified seven chief micro-organisms from the normal contents of the small intestine. Only two of them had any action upon proteids, the Streptococcus liquefaciens ilei and the Bacterium liquefaciens ilei; both liquefied gelatine and decomposed meat, evolving an odour of stale cheese but producing no indol or skatol. With the exception of the second mentioned, they all acted strongly on dextrose, five producing alcohol and six lactic acid. Frey found that one of these organisms, the Bacterium ilei, produced succinic acid, sarcolactic acid, alcohol, large quantities of carbonic acid gas, and of hydrogen. There is no doubt also that fats are acted on by some of the bacteria present in the small intestine, and are decomposed into fatty acids and glycerine, though there is little evidence to support the view that this decomposition occurs in health. Nencki, Macfadyen, and Sieber failed to find either leucin or tyrosin in the contents of the ileum, and thought that the explanation might be due to the lactic acid generated by micro-organisms so diminishing the activity of the proteolytic ferment of the pancreas that such a profound decomposition of the proteid molecule is prevented.

CHART X.—Showing the actual number of Bacterial Colonies grown from Segments of the Intestinal Canal of Salmon during different months.



Owing probably to the acid reaction of the contents, the so-called ptomaines have not been found in the contents of the small intestine under ordinary circumstances. Neither Brieger nor Baumann and Udransky were able to separate these bodies from the intestinal contents in healthy individuals, even twenty-four hours after death. The contents, however, contain bacteria which are able to produce ptomaines when grown upon gelatine, though, as said before, their growth in the bowel is inhibited in health by the acids present. Perhaps, also, the non-production of these poisonous bodies may be due to the antiseptic influences of the bile acids and to the diffusion of oxygen between the blood of the mucous membrane and the intestinal contents, although no free oxygen has ever been detected in them. The inhibitory action of the oxygen on these ptomaine-producing organisms is due to their anærobic conditions of growth—*i.e.*, they flourish best when oxygen is absent.

The usual method of estimating the amount of putrefaction present in the small intestine is by the estimation of the ethereal sulphates in the urine. In cases of intestinal indigestion, the putrefactive organisms are able to form many of the poisonous and non-poisonous derivatives of proteids, many of which belong to the class of ethereal sulphates. Any of the measures taken to diminish this putrefaction, such as the administration of antiseptic drugs or the giving of a purely milk diet, at once diminish these bodies in the urine. Stern (*Zeitschrift f. Hygiene u. Disinfections Kranchestus*, xii. s. 88) notes that observations on the number of organisms actually grown from the intestinal contents are of little value, owing to the fact that even under normal conditions their number varies much. Microscopically also an enormous number of bacteria may be observed, while only a few may grow on gelatine culture. Taking into consideration this fact, the estimation of the amount of decomposition in the small intestine is perhaps better arrived at from the amount of the products formed by bacteria and passed in the urine.

On the other hand, Gilbert and Dominici (*Compt. Rend. Soc. de Biologie*, April 1894) found that the micro-organisms in the fæces fell to $\frac{1}{71}$st of the previous number in man when fed on milk alone. Similarly, they found in the dog on a milk diet a great decrease in the numbers present in all parts of the alimentary canal—viz.,

TABLE XLV.

Stomach - -	100 pro milligramme, instead of			50,000
Duodenum -	50	,,	,,	30,000
Ileum - -	1300	,,	,,	100,000
Large Intestine,	1275	,,	,,	30,000

Rovighi (*Ztschrft. f. phys. Chem.*, xvi., 1/2, s. 20) found that he could diminish the ethereal sulphates in the urine of the dog to a marked degree by the administration of turpentine or camphor, but that the effect of these drugs was not nearly so pronounced in man. Mineral waters, such as Carlsbad or Marienbad, increased the output of sulphates in the first twenty-four hours, while after that they were diminished in quantity. He recommended kefir, a fermentation product of milk, as the best means of subduing intestinal putrefaction, ascribing its action to the lactic acid which it contains. An interesting observation was made by Mester (*Zeitschrift f. klin. Med.*, xxiv., 5/6, s. 441), who, in a series of experiments, excluded all chlorine from the food given to dogs. In a short time he found that the hydrochloric acid in the stomach disappeared, and that, with a meat diet, decomposition of the intestinal contents soon set in, with coincident increase of the sulphates in the urine, although if the diet given was poor in organisms no evidence of excessive decomposition could be found. If common salt was added to the meat diet the sulphates in the urine did not increase, showing that excessive decomposition of the contents of the alimentary canal had not occurred.

Chemical Poisons formed by Micro-organisms in the Alimentary Canal.—We have already seen (p. 186) that the digestion of proteids with the aid of the pancreatic ferment trypsin does not produce those poisonous alkaloids and bases which are commonly termed *ptomaines* (πτῶμα, a corpse) or *leucomaines*, when its action takes place under *strict aseptic conditions.*

Some of the final products of aseptic tryptic digestion consist of the amido-acids, tyrosin, leucin, and asparagin, and of the pigment tryptophan. Many bacteria are able to decompose the proteid molecules still further, although the first stages produced by their action are very similar to those produced by trypsin, *i.e.*, albumoses and peptones are formed. Later on, the amido-acids, fatty acids, carbonic acid, ammonia, amines, and in some cases, indol and skatol, result from their activity.

Ptomaines are compound ammonias, ammonias in which the hydrogen atoms are replaced in part or altogether by radicals. The simpler forms are amines. Thus in trimethylamine all the hydrogen atoms in ammonia are replaced by the radical methyl, thus:

$$N\begin{cases} H \\ H \\ H \end{cases} \qquad\qquad N\begin{cases} CH_3 \\ CH_3 \\ CH_3 \end{cases}$$

Ammonia. Trimethylamine.

The next class are diamines, in which the hydrogen atoms are replaced by two radicals in place of one, as in:

$$\begin{array}{l} CH_2 - CH_2 - NH_2 \\ \,| \\ CH_2 - CH_2 - NH_2 \end{array}$$

Tetra-methylen-diamine or Putrescin;

or with an additional radical, as:

$$\begin{array}{l} CH_2 - CH_2 - NH_2 \\ \,| \\ CH_2 \\ \,| \\ CH_2 - CH_2 - NH_2 \end{array}$$

Penta-methylen-diamine or Cadaverin.

Some of these bodies are not very poisonous, but bases with highly toxic properties can easily be formed from them. Thus piperidin may be procured from cadaverin, neurein from cholin; both exquisitely poisonous, although the mother substances possess little physiological action.

Another base possessed of highly toxic properties has been separated by Brieger from putrid horse-flesh four weeks after the commencement of decomposition. It appears to be an oxidation product of creatin, thus:

$$\begin{array}{l} \;NH_2 \\ / \\ C(NH) \\ \backslash \\ \;NH - CH_2 - CH_2 - COOH \end{array} \quad + 3O = \begin{array}{l} \;NH_2 \\ / \\ C(NH) \\ \backslash \\ \;NH - CH_3. \end{array} \quad + H_2O + 2CO_2$$

Guanidin-propionic acid (creatin). Methyl-guanidin.

Methyl-guanidin, therefore, is represented by $CH_3NH - C = (NH) - NH_2$.

Table XLVI.—*The better known Animal Alkaloids.*

Non-oxygenous:

Neuridin,	$C_5H_{14}N_2$	- - -	Non-toxic.
Saprin,	$C_5H_{14}N_2$	- - -	Non-toxic.
Cadaverin,	$C_5H_{14}N_2$	- - -	Slightly toxic.
Putrescin,	$C_4H_{12}N_2$	- - -	
Mydalein		- - -	Highly toxic.
Methyl-guanidin,	$C_2H_7N_3$	- - -	Toxic.
Piperidin,	$C_5H_{11}N$	- - -	Highly toxic.

Oxygenous:

Neurin,	$C_5H_{13}NO$	- - -	Toxic.
Cholin,	$C_5H_{15}NO_2$	- - -	Non-toxic.
Muscarin,	$C_5H_{15}NO_3$	- - -	Toxic.
Mytilotoxin,	$C_6H_{15}NO_2$	- - -	Toxic.
Betain,	$C_5H_{13}NO_3$	- - -	Non-toxic.

A distinction has been drawn between the animal alkaloids produced by the action of bacteria and those basic bodies arising from the metabolic processes of the body. The first are termed ptomaines, the second leucomaines. Many of the leucomaines belong to the uric acid series, as xanthin, hypoxanthin, adenin, etc.; they are non-toxic. Other leucomaines are recognised as being connected with creatin—such as creatinin, xanthocreatinin, crusocreatinin, etc.; they are toxic. The monamine trimethylamine is also found in the body, and a number of amido-acids, as leucin and tyrosin, which may be also classed under the term of alkaloids.

The simpler compounds formed in the intestinal canal, when the putrefactive processes do not exceed their normal limit, the amido-acids, the skatol, indol, and phenols, are derivatives of that portion of the proteid molecule which corresponds in arrangement to the bodies comprised in the fatty series. When true putrefactive decomposition of proteid bodies occurs, basic bodies, very similar to the alkaloids found in plants, are formed. The substances derived from animal proteids by the action of bacteria differ, however, from the corresponding vegetable alkaloids, in that they belong to the series with a molecular arrangement which characterises the fats; the majority of the vegetable alkaloids, on the other hand, have an arrangement of atoms based on the formula of pyridin.

The vegetable alkaloids have very similar properties. In conina, the alkaloid of hemlock, two atoms of hydrogen in ammonia are replaced by N_4H_7, thus—

$$N\begin{cases} C_4H_7 \\ C_4H_7 \\ H \end{cases} = C_8H_{15}N;$$

or in nicotine, where all three atoms of hydrogen are replaced by the triatomic N_5H_7, and whose molecule corresponds to two molecules of ammonia: $2N(C_5H_7)_2 = C_{10}H_{14}N_2$.

The compounds of the vegetable alkaloids correspond to salts of ammonia, not of ammonium—that is, they combine directly and do not lose the atoms included in the molecule of water.

Morphina $= C_{17}H_{19}NO_3$. Hydrochloride of morphia, $C_{17}H_{20}NO_3Cl$.

The mucous membrane of the bowel appears to constitute one of the bulwarks which defend the animal organism from outward infective agents. Thus Charrin (*Archives de Phys.*, 1896) showed that the toxines produced by the growth of bacteria rapidly lost their poisonous properties if introduced into an isolated loop of intestine, although their direct injection into the portal vein was followed by toxic symptoms. After destruction of the mucous membrane of the bowel by heat or by the action of tannic acid, they lost none of their toxic power when introduced into the intestinal loop. Charrin also found that the toxic symptoms produced by the injection into a vein of some of the contents of the ileum could be inhibited by the previous administration of an extract of the mucous membrane of the bowel.

CHAPTER XI.

The Influence of the Nervous System upon the Actions of the Digestive Organs.

Influence on the Salivary Glands—Secretory Fibres—Pressure of Secretion —On Gastric Digestion—On Pancreatic Secretion—On the Biliary Excretion—Intestinal Digestion—Paralytic Secretion—Summary.

Most of our knowledge with regard to the influence of the nervous system upon the digestive organs has been gained by the study of the processes occurring in the salivary glands, by reason of their superficial and exposed position. Lately, however, many observations of great interest have been made upon the nervous mechanism of both the gastric and the pancreatic secretions.

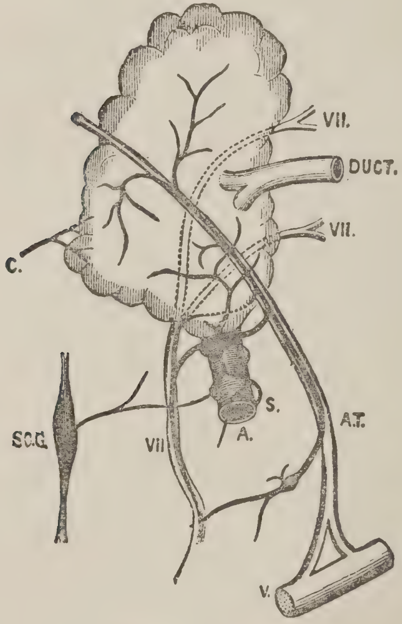
The Influence of the Nervous System on the Salivary Glands.—All the salivary glands are supplied with nerve fibres from the brain directly, and from the sympathetic system (see Fig. 32). These fibres are of three classes—secretory, vaso-constrictor or vessel-contracting, and vaso-dilator or vessel-dilating; the first and third of which are contained, as a rule, in branches of the nerves proceeding directly from the brain. These branches are the chorda tympani to the submaxillary and sublingual glands, and the auriculo-temporal, which communicates also with the otic ganglion, to the parotid gland. The second class, the vaso-constrictors, run in branches from the sympathetic system, along with some secretory fibres.

Ludwig (*Zeitschrift f. rat. Mediz.*, N.F., p. 259), in 1851, showed that if one of the cranial branches supplying a salivary gland is stimulated, two actions are produced, namely, secretion, and dilatation of the blood-vessels. These two actions, however, are not produced by the same fibres, as was proved

later, when it was shown that such drugs as atropine paralyse the secretory fibres, leaving the vaso dilators intact. If the filaments from the sympathetic are stimulated the blood-vessels of the glands contract, and a small quantity of saliva is secreted

FIG. 32.

DIAGRAM OF THE NERVE SUPPLY TO THE PAROTID GLAND.



(Meade Smith, after Yeo.)

AT, Auriculo-temporal nerve arising from *V*, the inferior branch of fifth cranial nerve. *SCG*, superior ganglion of the sympathetic nervous system in the neck, sending a branch to carotid artery (*S*) and thence to gland. *VII*, Portio dura of the seventh nerve.

which differs physically and chemically from that obtained on stimulation of the cerebral nerves. Heidenhain later advanced the proposition that there were two sets of secretory fibres—one dealing simply with the secretion of water, the other, to

which he gave the name of the metabolic fibres, with the secretion of the chemical bodies contained in the salivary juice. He also ascribed the conversion of insoluble into soluble substances and the increased production of protoplasm to the action of these metabolic fibres.

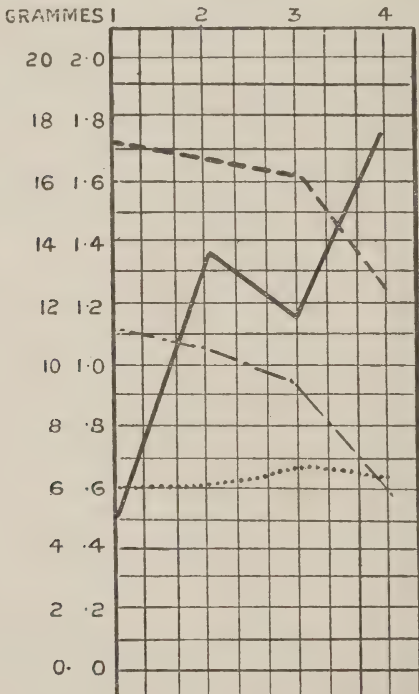
If a canula be placed in Wharton's duct, which leads from the parotid gland into the mouth, and the saliva is collected, its flow is found to increase on stimulation of the peripheral end of the divided chorda tympani nerve, though the saliva is very much more watery. At the same time, the blood-vessels of the gland become dilated. The action of atropin, above referred to, in causing dilatation of the vessels with a diminished flow of saliva, shows that the increase following on stimulation of the chorda is not due to increased blood pressure. Indeed, it has been found that the maximum pressure in the salivary duct may much exceed the blood pressure in the arteries during stimulation of the chorda. Thus in one experiment the blood pressure in the carotid of a dog was only equal to 125 mm., while the pressure in Wharton's duct reached 195 mm. of mercury. The dilatation of the blood-vessels may be looked upon as an instance of the general law that an organ when active always receives more blood than when it is in repose, to make up for the increased activity of its cells.

Chauveau states that the quantity of blood which passes through the carotid of a horse during mastication may be four times that which obtains when it is not feeding. (Chart XI.)

The endings of the secretory fibres of the chorda in the gland are as yet undiscovered; they probably, however, come in direct connection with the secreting cells themselves. Nerve fibres have been shown to end in the cells of the so-called salivary glands of the cockroach. The action of nicotin, which paralyses nerve cells much more readily than nerve fibres, has been employed to demonstrate the fact that many of the fibres of the chorda become connected with ganglion cells inside the submaxillary gland. Stimulation of the nerve, after the injection of nicotin into the local venous supply between the brain and the gland, produces no effect; although a similar stimulation of the gland itself is followed by a copious flow. The same has been found to hold good with regard to the vaso-dilator fibres. The stimulation of the sympathetic fibres, as has been said above, after division of the main trunk of the sympathetic nerve in the neck and moderate stimulation of the part connected with the glands, produces a thick viscid and scanty flow from both the submaxillary and sublingual ducts, the current of blood passing through these glands being at the same time diminished. From the parotid no visible secretion may escape, but on microscopical examination of the

gland its fine ducts will be found to be filled, or, as Langley expresses it, plugged with a thick secretion. If both the chorda and sympathetic nerves are stimulated, the action produced by the first, if the sympathetic be only moderately

CHART XI.—Showing the Decrease of Solids in the Submaxillary Saliva of the Dog on prolonged Stimulation of the Chorda Tympani. (Ludwig and Becker.) The curves are plotted for four equal periods after the commencement of stimulation.



Total Saliva Secreted.
Total Solids.
Organic Solids
Inorganic Salts
} Ten times the scale.

stimulated, prevails to such an extent that the submaxillary saliva is secreted in considerable quantity, but it is not so watery as when the chorda has been stimulated alone. Strong stimulation of both nerves causes a plentiful and dilute secretion.

TABLE XLVII.—*Parotid Saliva obtained by Stimulation of Jacobsen's Nerve.*

	Without.		With simultaneous stimulation of the sympathetic.		Percentage of Difference to first figures.
Water	99.44		97.58		
	98.97		98.26		
	99.43		99.36		
	99.51				
		99.339		98.40	−0.94
Total Solids ..	0.56		2.42		
	1.03		1.74		
	0.57		0.64		
	0.49				
		0.661		1.60	+142
Organic Solids ..	0.24		2.06		
	0.76		1.41		
	0.21		0.38		
	0.16				
		0.342		1.283	+275
Inorganic Solids ..		0.319		0.317	−0.6

TABLE XLVIII.—*Percentage Composition of the Saliva of the Cat, on Stimulation* (1) *of the Chorda Tympani*, (2) *of the Sympathetic.*

	Water.	Total Solids.	Organic Solids.	Inorganic Solids.	Percentage of Ash to Total Solids.
1. Stimulation of Chorda ..	98.795	1.205	0.865	0.339	28.1
2. Stimulation of Sympathetic—					
a. Weak	99.205	0.795	0.353	0.442	55.6
b. Stronger	99.299	0.701	0.426	0.275	39.2
c. Strong, after 5 mgrms. of Atropin	99.021	0.979	0.525	0.454	46.3
Difference of 1 from 2*a*	−0.41	+0.41	+0.512	−0.103	
Percentage Difference from 1 ..		+34	+59.1	−30 3	

The Influence of the Nervous System on Gastric Digestion.— The influence of the nervous system on the gastric glands appears to be exerted in two distinct ways. The secretion of gastric juice can proceed when all the nerve branches going to the stomach have been severed, although stimulation of the divided nerves influences it. There must, therefore, be a

peripheral secretory mechanism, capable of independent action, as well as a central apparatus. Heidenhain has suggested, indeed, that the flow of juice which follows direct mechanical irritation of the lining membrane of the stomach may, like the analogous phenomenon in Drosera, be independent of nervous control. Again, when the œsophagus is entirely occluded, as by a contracted scar (Richet), or disconnected, as by division in dogs (Pawlow), the presence of food in the mouth, or even the sight or smell of food, is sufficient to cause a flow of gastric juice. After both the nerves which run from the brain to the stomach, the two vagus nerves, and the sympathetic fibres also supplied to it, have been divided below the branches of the vagi, which go to the heart and lungs, the entrance of food into the stomach induces secretion and dilatation of the gastric vessels. Leubuscher and Schäfer (*Centralblatt. f. Innere Med.*, xv. 33) could find no alteration, after section of the vagi, in the contents of the stomach of a rabbit fed on milk, except that the stomach-wall was slack and dilated, the result probably of some disturbance of motility. A similar observation on the dog seemed to point to the absence of any disturbance of secretion, but to an altered motor-power.

All the evidence at present in our possession fails to prove the existence of true secretory nerves for the stomach, but the fact that the secretion can be influenced reflexly from the mouth, or by the character of the stimulus applied to its mucous membrane, and the circumstance that mental conditions can affect it markedly, go to show that, however independent of central control the gastric secretory mechanism may be, the greater nerve centres possess some power over it, although they may be seldom called upon in health to exert it.

The reflex impulse from the mouth to the gastric glands has been shown by Pawlow and Schumowa-Simanowskaja in dogs, in whom the œsophagus was divided, to be interrupted by section of the vagi. When these nerves were divided, the passage of food through the mouth and out at the open part of the gullet caused no reflex secretion of gastric juice. These observers maintain that the negative results of others have been due to coincident circumstances, such as the influence of the narcotic or anæsthetic given, etc., because they could assure themselves of the occurrence of a secretion of gastric juice on irritation of the peripheral parts of the vagi divided as above described.

In curarised fasting dogs Schneyer ligatured the œsophagus in the neck, doubled the duodenum back against the stomach, divided both the vagi, and obtained the following results on the electrical stimulation of the vagi

and splanchnics. Stimulation of the vagi in the neck when undivided, or of their peripheral portions, caused a flow of gastric juice. The secretion began at once, but was most marked 7 to 10 minutes after stimulation. Stimulation of the central portions of the vagi or of either portion of the splanchnic nerves caused no secretion.

In dogs deprived of food by the mouth for 48 hours, but given nutrient enemata, the fluid secreted by the gastric glands on stimulation of the vagi contained free hydrochloric acid and inorganic chlorides, and possessed active peptic properties.

Hayem and Winter suggested that at the commencement of the act of secretion after the ingestion of food the gastric glands only afforded a solution containing inorganic chlorides, while the stimulation of the food on the mucous membrane caused a subsequent liberation of hydrochloric acid from the cells in place of the salts. Schneyer holds that stimulation of the secretory mechanism by food or other means induces a flow of chlorides from the blood into the gland cells, while the cells through their specific action secrete the corresponding acid.

By an ingenious application of the X-rays and the addition of small portions of sub-nitrate of bismuth to the food, Roux and Balthazard have been able to observe the movements of the stomach in frogs and in dogs. They have found that the functions of the stomach in both animals are identical. The food accumulates in the greater curvature. No movements of the walls could be seen in this part.

The pyloric region exhibited marked peristaltic movements and is regarded by these observers as the true motor agent of the stomach. They have been able to show that the movements of the walls close to the pylorus are due to the active peristalsis of the neighbouring parts, contrary to Hofmeister and Schutz's views, and corroborate Moritz in stating that the presence of food in the duodenum does not arrest the prepyloric peristalsis.

The Influence of the Nervous System on the Pancreatic Secretion.—As in the submaxillary gland, section of all the nerve fibres going to the pancreas is followed by a "paralytic" secretion of a thin, watery juice. Electrical stimulation of the part of the brain known as the medulla oblongata causes the gland to commence secreting if inactive, and increases its secretion if it is actively secreting at the time. Stimulation of the central end of the vagus, the part going to the brain, or of any sensory nerve, arrests pancreatic secretion even for some time after the stimulation has ceased, possibly through contraction of the blood-vessels. When food is taken into the stomach the pancreatic secretion at once com-

mences, while if ether be injected into the stomach of an animal with a pancreatic fistula secretion is at once set up, corresponding in character to the time which has elapsed since food was taken, viscid if within six hours, watery if fifteen hours, after a meal. The available evidence as to the influence of nerve fibres on the pancreatic secretion is little if at all more conclusive than that relating to the gastric secretion, and consists of very similar facts. Actual experiment fails to reveal positive proof of the existence of vasomotor nerves of the pancreas, but the reflex secretion following upon ingestion of food and stimulation of the stomach, and the "paralytic" flow on section of all the pancreatic nerves, suggest the presence of some central nervous control. Some recent observations, which, however, require further corroboration before they can be absolutely accepted, tend to show the existence of nerve fibres in the vagi (Popielski, *Centralbl. f. Phys.*, x. s. 405, 1896) of the dog, some of which excite while others arrest pancreatic secretion. This observer induced a flow of juice by introducing some 5 per cent. hydrochloric acid solution into the duodenum, or by using pilocarpine, and then arrested the secretory action produced by this drug by stimulation of the vagus. The latent period before this action took effect was from 5 to 7 seconds. Popielski considers it probable that a reflex centre for the control of the different secretory apparatus adjacent to the pyloric end of the stomach is situated in the neighbourhood of the pylorus.

Shirokikh found that local stimulation of the stomach with mustard oil or cayenne pepper did not induce a flow of pancreatic juice in dogs unless large enough doses were given to cause vomiting; while Dolinsky, experimenting on dogs in whom both pancreatic and gastric fistulæ had been made, found that weak mineral acids, acetic and lactic acids, and sour drinks reflexly induced the secretion both of the gastric and pancreatic juices. Alkalies caused a flow of gastric secretion but no flow from the pancreas until the gastric juice had altered the reaction, or unless gastric secretion had been previously induced. When the œsophagus was cut through in addition to the establishment of the fistulæ, the excitation of the pancreas was only indirect—*i.e.*, induced by the flow of acid gastric juice, following the law that acid fluids call forth alkaline secretion. The secretion from the pancreas followed the ingestion of fats; alcohol brought about only a moderate flow.

The Influence of the Nervous System on the Secretion and Expulsion of the Bile.—Bile is constantly secreted, although only expelled into the duodenum at intervals. Thus the

influence of the nervous system may affect it in two ways—by influencing the secretion or the expulsion of the bile. As the amount of bile is closely connected with the quantity of blood passing through the liver, and as this is dependent upon the blood-supply of the other abdominal organs, any condition which constricts the abdominal vessels will slow bile secretion. In this way stimulation of the central brain centres, the spinal cord, the splanchnic nerves, and any sensory nerve diminishes its formation. Section of the cervical spinal cord, by lowering the general blood-pressure, acts similarly, but section of the splanchnic nerves, causing dilatation of the abdominal vessels without a marked decrease of general pressure, increases biliary secretion. No evidence exists as yet as to the existence of any special nervous mechanism, local or central, governing the secretion of bile. When the spinal cord is stimulated the muscular fibres of the gall-bladder and the larger bile-ducts contract, and expel the bile contained in them. The natural expulsion of bile which occurs on the entrance of the acid contents of the stomach into the duodenum is probably due to a reaction, similar to that following stimulation of the spinal cord, reflexly induced by impulses from the duodenal mucous membrane. The passage of food into the stomach leads to an increase of secretion (Chart IV.), the presence of the food in the duodenum to expulsion.

Intestinal Secretion.—The influence of the nervous system on the secretion of the intestinal mucous membrane has been very fully investigated, and these investigations have yielded more fruitful results than those performed in connection with the stomach and pancreas.

Stimulation of the vagi was found by Thiry to have no effect on the secretion, while Budge and Lamansky observed an increase after removal of the cœliac and mesenteric nerve plexuses. Lauder Brunton, Pye-Smith, and Moreau isolated three contiguous segments of the small intestine of the dog with ligatures, and divided all the nerves going to the middle segment. In a short time this middle portion was distended with secretion, while the other two remained empty. The absence of secretion in the segments with intact nervous supply must have been due to a nerve mechanism capable of restraining secretion, and Brunton located this mechanism in the lower ganglia of the solar plexus and in the superior mesenteric branch from these ganglia. Destruction of the ganglia, though

the other nerves be intact, causes secretion, while if they are left untouched, removal of the spinal cord and semilunar ganglia, and section of the vagi and splanchnics, fail to produce it.

The movements of the intestinal wall in the rabbit are not influenced by section of the vagi or splanchnic nerves (Pohl), but can at once be stopped by stimulation of the mesenteric nerves, unless the causal irritation is very powerful, or when this has been locally produced. Judging by the effect of local irritants on the muscular tissue of the walls, the mucous membrane of the small intestine is very insensitive.

The plexuses of Auerbach and Meissner (cf. p. 106) are formed of ganglion cells, each with an axis-cylinder process and many protoplasmic offshoots. Fine varicose fibres, which Dogiel (*Anat. Anzeig.*, x. 16, s. 517) regards as derived from the cerebro-spinal system, form networks round the ganglia. The recent neuronic theory of the relationship of one cell or neurone with another, in which all actual direct connection between them is denied, may be applicable to these ganglionic plexuses, as it seems to be reasonable when applied to the cerebro-spinal system. Under these circumstances the neurones composing the plexus may be regarded as capable of communicating impulses one to another, while each transmission must at the same time cause some slight change in the adjacent terminations of the neurones in communication with the central system or with the larger sympathetic centres, insufficient under ordinary circumstances to cause a transmission of the impulse to the higher neurones forming the connection between the cord, or brain, or sympathetic centre, and the neurone in juxtaposition to the intestinal ganglia. Forcible impulses from the neurones forming the intestinal plexuses, or from the central neurones, are able, on the other hand, to modify the action of the terminal members, central or peripheral, of their chains. When the innervation of the stomach and intestines is regarded in the light of this theory the difficulty arising from the frequent isolated action of local ganglionic systems, if looked upon as being in direct unbroken communication with the higher centres, is surmounted. Each nerve-cell with its processes is an individual isolated unit or neurone, while its fine terminal processes, round the cell at one extremity and given off from the axis cylinder at the other, interlock with and closely adjoin the fine branches of other neurones, but principally with that one forming a link in the neurone chain of communication. It is more probable, however, that the ganglia of the intestinal plexuses communicate directly with one another, but are only connected by neuronic intercommunication with the cerebro-spinal centres.

If this suggested arrangement of the nervous supply of the alimentary canal be accepted in rough detail, the continuous actual inter-communication of the nerve elements composing the two plexuses will explain the transmission of impulses, inhibitory or exciting, from one segment of the tract to another,

which we have seen constantly occurs during the course of normal digestion. That this may be so is the more probable because any abnormal change in one part of the canal speedily leads to sympathetic changes in another. If there be intestinal discomfort gastric digestion suffers; while often diarrhœa may be produced when irritating matters have been swallowed, although vomited before any part could have reached or been re-excreted into the bowel.

During the course of the healthy digestion of a good meal the associated nerve elements in the intestinal walls give no sign to their host as to what is going on; unless it be that the contiguous neurones signal to the brain the general feeling of satisfaction locally pervading the presiding nerve cells, to mingle with the similar message directly impressed by more purely chemical means on the brain cells by reason of the absorption of food products into the blood-stream.

But if too much or too rich food be eaten, or it may be too often, the normal stimulation of the local apparatus passes into irritation, raising sufficient energy for the transmission of a warning message to the neurones contiguous to it, and thence to the central system; although owing to the line of least resistance lying along the joined ganglia the message, by the time it reaches the brain, is frequently indefinite and diffuse. An intense pain, as that caused by a gastric ulcer, may be able to telegraph its exact site, but even in such a case there is great uncertainty. The slowly increasing pain of subacute appendicitis signals most contradictory messages, until it has become sufficiently acute to influence predominantly those central neurones connected with the spot affected. Such a rough hypothesis, however, requires qualification in so far that the spinal cord appears to contain centres inhibiting the excessive peristalsis of the intestinal walls, not only in the splanchnic centre but in the lower part of the cord. Thus section of the cord below the splanchnic centre causes the peristalsis produced by stimulating the vagi to become greater, and after removal of the lower dorsal and lumbar sections of the cord the bowel only exhibits a "pendulum-movement" (Pal) unaltered on dividing the splanchnic nerves, while stimulation of the vagus causes strong peristaltic movements, which can be arrested by stimulation of the peripheral part of the splanchnic nerve. The vagi appear to supply motor fibres to the bowel as far down as the rectum, the splanchnics,

and other nerves from the cord, inhibitory fibres throughout the same extent.

Such experiments, however, only apply to conditions in which the stimuli applied are much greater than probably occur in a normal state of digestion, with the exception of the inhibitory property of the spinal cord centres. If the neurone theory is applied here, it may feasibly be postulated that the neurones connected with these spinal centres are constantly charged with messages providing that the partly independent ganglionic system shall not excite too great a peristaltic movement of the bowel wall at the instance of the vagus nerves.

Moreau, in 1868, maintained that the fluid obtained from a loop of bowel, all the nerves of which had been severed, was identical with the normal intestinal secretion. Others since that time have regarded it as a so-called "paralytic intestinal juice," a transudation not a secretion. Mendel lately has shown that Hanau, Lauder Brunton, and Pye-Smith are correct in looking upon the fluid as being the result of a true secretion, and, contrary to Leubuscher and Tecklenburg, has found that it possesses an amylolytic power, and can form dextrose from cane-sugar and maltose, though inactive towards lactose.

Courtade and Guyon (*Arch. de Physiologie*, 1897, p. 422), by using an apparatus devised to register the contractions of the circular and longitudinal muscular fibres in the wall of a segment of the bowel of the living dog immersed in warm physiological salt solution, found that normally the circular fibres acted more effectively in causing peristalsis than the longitudinal. Their action was synchronous, while the contractions of one of the layers followed an upward, of the other a downward direction. Stimulation of the large splanchnic nerve arrested peristalsis for a moment owing to paralysis of the longitudinal fibres, whether the peripheral or the central stump of the nerve was irritated. The circular fibres were only affected when the stimulation of the nerve was slight. Section of both vagi did not alter this result. Very energetic electrical stimulation of the splanchnic in a few instances caused contraction of the longitudinal and paralysis of the circular fibres, and was accompanied by vaso-constriction of the blood-vessels in the walls of the intestine.

The sympathetic nerves, therefore, are concerned in the regulation of intestinal peristalsis, and can act on it directly or reflexly.

CHAPTER XII.

A Comparative Study of Digestion in Animals.

Types of Nutrition — Vegetal — Saprophytic — Specialised — Protozoa—Amœba—Foraminifera—Metazoa—Spongida—Cœlenterata—Annuloida—Arthrozoic Series—Arthropoda—Crustacea—Polyzoa—Mollusca — Gasteropoda—Tunicata—Summary—Digestion in Pisces—Organisms in Canal—The Salmon—In Aves—In Reptilia—In Ruminantia—In other Herbivora—Vomiting—Digestive Leucocytosis.

We have now to trace the gradual ascent manifested in the phenomena of digestion in the lowest and most general form in unicellular animals, towards the complexity of the process as it occurs in man. All animals, even the lowest and least specialised, may be divided into herbivorous, carnivorous, or omnivorous forms. No sharp line of demarcation can be drawn between the animal and vegetable kingdoms with regard to digestion. The lowest animal forms (of the class *Gregarinidæ*) practically obtain the elements necessary for their existence in the same manner as the *Bacteria*.

Although the lowest forms of animal life resemble each other in the minuteness of their bodies and the simplicity of their structure, they by no means invariably present evidences of uniform digestive processes. Indeed, throughout the whole animal kingdom, three chief types of nutrition may be identified—

1. Vegetal.
2. Saprophytic.
3. Animal.

1. *Vegetal nutrition.*—In some animals chlorophyll is contained in the cells, and serves in them, as in vegetable forms, a nutritive purpose as well as a respiratory one. Chlorophyll is found chiefly among the *Flagellata.* In them the digestive

organs are called chromatophores, and consist of granular masses of protoplasm tinted by a colouring substance.

2. *Saprophytic nutrition* is the simplest type, and occurs in the *Gregarinidæ*, *Protoplasta*, etc. The organism absorbs its food through any area of its outer surface, extracts those parts capable of yielding nourishment, and rejects the remainder.

3. In all animals, save those which come under the preceding types, the function of nutrition is served by a *specialised digestive canal*, which may be of the simplest or of the most complicated description, and by which the animal seizes its food and extracts the elements necessary for its life.

As we ascend the scale we pass from cells, forming complete organisms and endowed with many different properties, but performing the functions allotted to them in the most perfect manner with what appear to be most imperfect means, to animals in whom separate organs, made up of highly specialised cells, perform the work demanded of them in a more and more finished manner, although the single cell of the lowest is as competent to subserve the laws of life in its own singular person as are the different congeries of myriads of cells in the complicated beings, evolved in the process of time from those very units.

THE INVERTEBRATA.

The Gregarina.—This unicellular parasitic animal occurs in the alimentary canal of both vertebrates and invertebrates, especially, however, in the intestines of cockroaches and earthworms. It absorbs predigested substances from the alimentary canal of its host by every part of its surface, through which it can also excrete the effete matter. As it practically exercises no digestive function save the absorption of nutriment already prepared for its needs, it can hardly be said to digest, only to assimilate some of the food predigested by its host.

The Amœba.—The *Amœba* consists simply of a mass of living, contractile protoplasm with a nucleus. Miss Greenwood has investigated the process of digestion in *Amœba proteus* with great care, and has added largely to our knowledge of its life-history. An *Amœba* when in active movement progresses in a definite direction; a fairly constant hind end can then be distinguished. It is this part that most actively ingests. "The ectosarc is drawn like a funnel round the prey, and the opening which corresponds to the mouth of the funnel is

eccentrically closed." If the prey be in active motion when engulfed in the cell protoplasm of an *Amœba*, a considerable area of water surrounds it; if immobile, little fluid is included. This space within the protoplasm, or "vacuole of digestion," remains to a greater or less extent until full digestion is accomplished. The movements of the *Amœba*, which serve both for progression and for the prehension of food, are produced by temporary protrusions of parts of the cell protoplasm, termed pseudo-podia. The protrusion and retraction of these pseudo-podia initiate motion, while food particles too large to be directly drawn in are first enwrapped by pseudo-podia, and thus engulfed in the cell substance. The lateral pseudo-podia may sometimes engulf the prey, the anterior and most actively moving part never. The length of time which the act of ingestion lasts is comparatively short, generally not more than a few minutes.

Fat, pure carbo-hydrates, and innutritious substances, such as litmus, are rejected unaltered after ingestion. Starch grains, for example, remain for some days in the body of an *Amœba*, but when ejected are unchanged either in shape, size, or reaction. Unshielded proteid matter and proteid surrounded by a cellulose wall, is rapidly digested, although in the second case the cellulose covering is not dissolved nor visibly perforated. When protoplasmic food is enclosed by an *Amœba*, the "vacuole of digestion," mentioned above, persists until all the nourishment has been removed. If the food be such that the *Amœba* cannot digest it, the water occupying the vacuole soon disappears, and is not replaced by a digestive fluid, such as is secreted by the protoplasm under the former conditions. Engelmann, Meissner, and Favre-Domergue have thought that they could detect an acid reaction in the fluids of some *Amœbæ* during digestion, but Miss Greenwood was unable to corroborate these observations, either by means of methyl-violet or tropæolin. The actual agent employed is unknown, but it appears likely that in *Amœba* the digestion of proteids is carried on by an acid and a ferment, as in so many other animals. Metschnikoff has noticed, in the course of his work on the phagocytic power of various *Amœbæ*, that the bacilli killed by them do not change their shape, although they react to stains in a totally different manner than when living. For instance, they acquire the power of taking up vesuvin, which does not affect them in their natural condition. The digestive

power of the *Amœbæ* is their chief defence from their enemies, and by it they are able to protect themselves and to obtain their food at one and the same time.

Speaking of the *Rhizopoda*, to which family the *Amœba* belongs, M. Richet says that "irritability is their life complete." The presence of particles of food irritates the protoplasm of the cell, excites digestion and absorption, and causes the rejection of innutritious material. The life-history of the *Amœba* provides a practical illustration of the unaided powers of *Protoplasm*. In those members of the order of *Amœbæ* in whom the body is protected by a carapace, ingestion is carried on by the portion uncovered by it, the process being identical with that in the forms in which the body is naked.

The members of the *Foraminifera* may be regarded as complex *Amœbæ*, united together and enclosed in a shell. When the shell is perforated, the food is seized and taken in by the pseudo-podia protruded through the apertures; when imperforated, by the pseudo-podia of the youngest and as yet uncovered segment.

The *Infusoria* show a marked advance on the conditions so far described. They possess a mouth and a distinct but short œsophagus, which does not end in any gastric dilatation, but is simply a closed tube. Particles of food are brought to the oral aperture by means of flagella (*Infusoria flagellata*), tentacles (*I. tentaculifera*), or cilia (*I. ciliata*). In *Monas vulgaris* the food is dashed against the mouth by a sudden jerk and pressed into it by the base of the flagellum, a whiplike process. In *Infusoria ciliata* a further differentiation of the alimentary canal can be traced, as it possesses an anal region, which is, however, not directly connected with the œsophageal tube. No actual anal aperture is present except when effete matter is ejected, but this always takes place at one well-marked region. In *Paramœcium* (see Fig. 33) the particles of food are carried round the body of the organism in vacuoles of the endosarc, or inner part, by contractile movements of the ectosarc, or outer part of the protoplasm. Digestion goes on during these movements, and the products are absorbed by the contiguous protoplasmic substance.

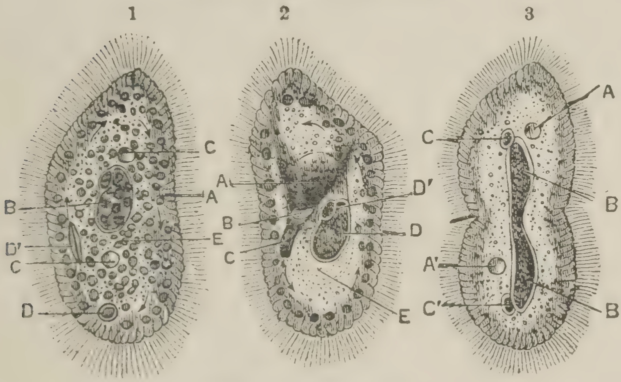
In the *Protozoa*, digestion is endosmotic in the *Gregarinidæ*, in the other classes true digestion of solid particles is performed by the entire cellular body, while there is a gradual advance from the *Amœba*, where the points of entry and exit

of the food are not clearly marked, to the *Infusoria*, with an œsophagus and, in some, a distinct anal region.

When we turn from the *Protozoa* to *Metazoa*, or many-celled organisms, we find that the *Spongida*, or sponges, the lowest in the scale of the *Metazoa*, possess a body cavity which serves both for digestion and circulation. Water bearing food particles passes through minute pores on the surface of the body, circulates through the gastro-vascular space, and finds its way

FIG. 33.

PARAMŒCIUM BUSSARIA.



(Meade Smith, after Stein.)

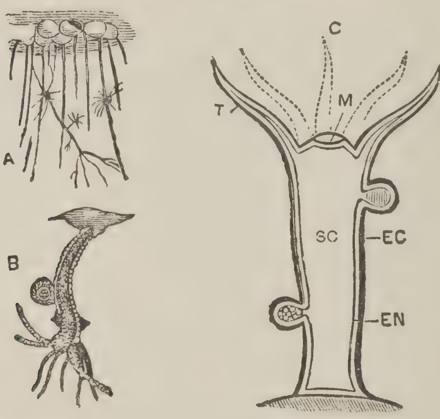
1. Viewed from the Dorsal side.
A, Cortical layer; *B*, Nucleus; *C*, Contractile vesicle; *D*, *D′*, Food particles; *E*, Chlorophyll.
2. Viewed from the Ventral side.
A leading to *B*, The mouth; *D*, Nucleus with nucleolus *D′*; *E*, Central protoplasm.
In 1 and 2 the arrows indicate the direction of protoplasmic flow.
3. Transverse division of *Paramœcium*.
A, *A′*, Contractile vesicles; *B*, *B′*, Nucleus dividing; *C*, *C′*, Nucleolus divided.

out again by a smaller number of larger apertures, or oscula, along with any effete products. The body cavity is lined with flagellate cells, which possibly have the power of digesting. It forms a rudimentary type of a true digestive system. The *Cœlenterata* differ from the sponges in having no inhalent or exhalent pores, while they possess a distinct oral aperture and a complicated gastro-vascular system, ending in an anal opening. The mouth communicates directly, or by a short canal,

with a dilated sac or stomach, from which numerous gastro-vascular canals, by which both the lymph and blood-vessels of higher animals are represented, run out to the margin of the body, to end in a peripheral, circular canal (see Fig. 34). The slimy secretion of *Medusæ* has been found not to contain any digestive action, but Krukenberg has observed the digestion of fibrin introduced into their body cavities. In *Actinozoa* the mesenterial filaments are said by the same observer to secrete an active digestive fluid. Probably the chief mode of digestion in *Cœlenterata* is intracellular, the cells of the inner layer

FIG. 34.

THE HYDROZOA.



(Meade Smith, after Jeffrey-Bell.)

A. Hydra viridis attached to Duckweed.
B. One of the same magnified.
C. Diagram of a section of *Hydra*. *EC*, Ectoderm; *EN*, Endoderm; *M*, Mouth; *SC*, Somatic cavity; *T*, Tentacles.

of the protoplasm digesting and absorbing the food, thus providing suitable nourishment for themselves and the other cells of the body.

In *Echinodermata* the digestive canal is further differentiated. It consists of a mouth, œsophagus, and an intestinal canal, in which there is no division into stomach and bowel, and which ends in an anal opening. The canal is suspended in the body or somatic cavity, and is distinct from the water-

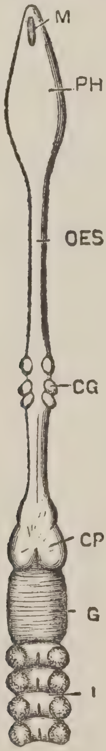
vascular and true vascular systems. In *Uraster rubens* Griffiths found no digestive ferment in the cells lining the tract, except in those forming the blind processes or pyloric cæca which run from the intestine along the rays. This ferment acts on oils, emulsifying and splitting them, converts starch into sugar, and digests albumin. The digested part of the food transudes through the walls of the canal into the somatic cavity, and is absorbed by the cells lining it.

The first class of *Annuloida* exhibits a reversion to a more rudimentary type of digestive apparatus, in accordance with the rule that true parasites have their digestion performed vicariously. The members of this class possess mouths and simple intestinal canals, generally without an anus. The *Cestoidea*, as shown by Fredericq, secrete no ferment of any kind, but absorb pre-digested material from the fluids surrounding them. The *Rotifera* form an exception as they are not parasitic. In addition to a simple but complete alimentary canal, many of them have a well-developed muscular pharynx and two glandular tubes opening into the anterior part of the stomach, which possess a pancreatic function. The second class of *Annuloida*, *Annelida*, includes the leeches and the earthworms. The leech used in medicine, *Hirudo medicinalis*, has a mouth armed with chitinous or horny teeth opening into a pharynx, which is provided with glands. The sucker at the anterior part of its body is brought into action by muscles surrounding the pharynx. A slender gullet passes from the pharynx into a long stomach, furnished with a number of lateral diverticula, from which a narrow intestine runs to a dorsally placed anus. The earthworm possesses a still more elaborate canal (see Fig. 35). A small opening forming the mouth leads into a cavity furnished with true salivary glands, which adjoins a pharynx. This passes into a straight œsophagus with three sets of diverticula or glands, and is continued into a crop or proventriculus about the fifteenth segment of the worm's body. This in turn opens into a muscular gizzard or stomach, which is succeeded by the intestine, terminating in an anus. The secretion of the salivary glands acts on starch but has no power of digesting proteids. The fluid poured out by the glands on each side of the œsophagus is rich in calcium carbonate, serves to neutralise the organic acids of the food, and thus aids the digestive fluids which are only active in alkaline media. The gizzard usually

contains small stones, and serves the same purpose as the gizzard in birds. A yellowish glandular tissue envelops the intestine and is called the liver, but it secretes a pancreatic

FIG. 35.

DIAGRAMMATIC REPRESENTATION OF THE DIGESTIVE ORGANS IN THE EARTHWORM.



(Meade Smith, after Ray Lankester.)

M, Mouth; *PH*, Pharynx; *OES*, Œsophagus; *CG*, Calcareous glands; *CP*, Crop; *G*, Gizzard; *I*, Intestine.

fluid, and must be regarded as the representative of the pancreas of higher animals, and not of the liver. Digestion in leeches and earthworms is essentially the same as pancreatic digestion

of vertebrates, and can proceed as far as the formation of amido-compounds.

Among the larger series of the *Metazoa* termed the Arthrozoic Series the digestive apparatus in the first class of *Nematoidea*, or "thread-worms," is very similar to those already described. The class *Arthropoda* comprises the animals usually known as insects, and the crustaceans. A general survey of the group will suffice. The majority of its members have well-defined digestive tracts. The mouth is provided with suckers, and organs for mastification, or organs for biting. The epithelium of the intestine is often furnished with a covering of chitin ($C_{15}H_{26}N_2O_{10}$), a hard, horny substance designed to crush the food. The lower arthropods have so-called livers, which are blind or cæcal prolongations of the intestine; the higher groups possess a "liver" of considerable size, especially *Crustacea*, though a better name for it is a "pancreas." The salivary glands are better marked as a rule in *Insecta* than in the other classes. The bee is provided with a cylindrical tongue which serves to lap up honey, and a crop, or honey-bag, separated from the stomach by a valve which must be opened by special muscular action before any of the contents can enter the stomach. In the bee's crop a change occurs in the nectar, which serves to arrest any acetic acid fermentation. On reaching the hive the nectar can be regurgitated into the wax cells prepared for it. The juice which is stored in the hives for the use of the larvæ has been found to be the regurgitated contents of the true stomach, the valve at its entrance being raised by muscular action to allow of their ejection. The food stored for the larvæ destined to become queen-bees is free from any admixture of pollen; the food of the drones contains pollen grains, partially digested, after the fourth day. The following table (Griffiths) gives the average composition of these food-stuffs :—

TABLE XLIX.—*The Food of Bees.*

		Food Stuff of		
		Female or Queen Bees.	Male or Drones.	Neuter or Working Bees.
Water		69.38 per cent.	72.75 per cent.	71.63 per cent.
Total solids		30.62 ,,	27.25 ,,	28.37 ,,
Per cent. of solids.	Nitrogenous	45.14 ,,	43.79 ,,	51.21 ,,
	Fats	13.55 ,,	8.32 ,,	6.84 ,,
	Glucose	20.39 ,,	24.03 ,,	27.65 ,,
	Ash	4.06 ,,	2.02 ,,	—

All these foods are rich in nitrogen. The queen-bee's food is the stickiest, that of the working-neuter the most fluid. The sugar present is always invert-sugar.

The web, by means of which the spider catches its prey and preserves its young, is produced by more than a thousand glands with ducts opening to the surface in six projections or mammillæ on the posterior part of the abdomen. The secretion is insoluble in water, and has a nitrogenous basis. The products of digestion in the insects and crustaceans are removed by the blood-vessels, chiefly venous in character, distributed over the outer surface of the intestinal canal. In many *Crustacea* the digestive organs are surrounded by cells filled with yellow or blue oils, which probably serve as stores of nutriment, to be used during the moulting season. The colouring matters in these oils are termed *lipochromes.*

The stomach of the fresh-water crayfish, *Astacus fluviatilis*, is much more complex than any of those hitherto described. The cardiac portion contains two hard nodules, or gastroliths, weighing about three grains each, imbedded in the walls. These are cast in summer with the carapace. This portion of the stomach is also furnished with minute hairs. In the pyloric half the walls are strengthened by calcified ossicles moved by four principal muscles which are attached to the carapace, and unite to form a powerful gastric mill. The walls of this part are also provided with long hairs which act as a strainer by preventing any coarse particles from entering the intestine.

The *Polyzoa*, though mainly microscopic, possess complete alimentary canals, with an anus opening close to the mouth. Absorption of the products of digestion, however, is conducted in a similar manner to that in *Actinozoa* and *Echinodermata*. The digestive tract is suspended in a somatic cavity, the products of digestion penetrate the visceral walls, and are absorbed by the cells lining the body cavity, or the organs situated in it. The *Brachiopoda* are characterised by a similar arrangement.

The Mollusca.—The order of *Lamellibranchiata* is characterised by an oral cavity supplied with cilia, a short œsophagus, an expanded stomach, surrounded by a so-called liver, and furnished near the pylorus with a crystalline style, and a long intestine, much convoluted, which passes through the heart and terminates in an anal projection. There are no salivary glands, and the so-called liver possesses the properties of a pancreatic gland. Fredericq claims to have isolated glycogen

from the "liver," but it is probable that it is only present during the periods of rapid growth when moulting. The contents of the digestive canal are acid, due to hydrochloric acid. This is especially the case in the contents of the stomach, and it is possible, as Griffiths suggests, that this is the first suggestion of a separate digestive act performed by the stomach. Absorption takes place through the medium of blood-vessels. In *Gasteropoda* the snail may be taken as the type. The mouth is bounded by lips, and is situated just in front of the foot. Two large salivary glands open into it. The œsophagus dilates into a crop leading to the stomach, which is provided with a blind cæcal appendage. A long and coiled intestine leads into a wider rectum, which opens into the mantle. Round the intestine is a large organ with many lobes called a liver, but exercising a pancreatic function. The ducts from this organ open into the stomach and anterior part of the intestine. The salivary fluid acts on starch, as does the secretion of the "liver," while the latter can also enable the digestion of proteids to take place in alkaline media.

The *Cephalopoda* present analogous features. Krause finds that their salivary glands secrete a poison with which they can kill crabs, etc., before they commence to eat them. When it is injected into frogs, these animals die.

The Tunicata.—The *Tunicata* have a mouth leading into a pharyngeal-respiratory chamber, from which the food particles are selected by small tentacles round the opening into the œsophagus and passed down to an internally-folded stomach. The intestine is covered with tubules, called Savigny's tubules, which may be present over the stomach wall as well. These tubules open by a common duct into the stomach, and appear to have a pancreatic function.

A general survey of the various facts relating to digestion as it occurs in the *Invertebrata* will not be out of place here. In the purely parasitic types, *Gregarina* and *Cestoidea*, no organs which subserve a digestive function have been discovered; they simply absorb and utilise pre-digested foods. The *Rhizopoda* ingest, digest, and excrete by their unicellular bodies in virtue of the properties of their protoplasm. Their digestion is absolutely intra-cellular. Some of the *Infusoria* may be able to secrete a digestive fluid which can act in the short œsophagus (*Paramœcium*), but the main digestive action occurs within the food-vacuoles which develop in the proto-

plasm. A slight advance takes place in the sponges, where the flagellate cells lining the gastro-vascular cavities act for the cells of the mesoderm, and possess the power of ingestion, digestion, and excretion of waste products, while the products of the digestion are transmitted to the rest of the body. These lining cells are able to form a ferment akin to that of the vertebrate pancreas, or, more correctly, to form three ferments—diastatic, proteolytic, and fat-splitting. Among the lower or Zoophytic members of the *Metazoa* the processes of digestion and absorption are performed in a manner very similar to the processes in *Rhizopoda* and *Infusoria*. They possess, however, gastro-vascular cavities lined with flagellate cells, into which the food particles pass through apertures in the body-wall, as in *Spongida*; or through a distinct oral aperture, as in the *Cœlenterata*, into a common digestive and somatic cavity. In the two divisions of the *Cœlenterata*, the *Hydrozoa* and the *Actinozoa*, a further advance is marked by the fact of digestion of food taking place in the fluid contained in the central cavity and absorption of the products by the endodermic cells. In the lower forms the food is brought directly into contact with the protoplasm of the cells, which exercises both a digestive and an absorptive action on it. In the *Echinodermata* the digestive canal is distinct from and suspended in the somatic cavity, and the products of digestion transude through the walls of the alimentary canal and are absorbed by the cells lining the somatic cavity. In the Annuloid Series, except in the lower parasitic members, the digestive apparatus is much more highly specialised, and is divided into a pharynx, a gullet, a stomach, an intestine, and an anal aperture. The leech possesses a stomach furnished with numerous diverticula; the earthworm, carbonate of calcium glands on each side of its œsophagus, a stomach divided into crop and gizzard, and a pancreas or so-called liver enveloping the bowel. The digestion of food is carried on in these species in an alkaline medium, and is capable of performing all the changes brought about by the pancreatic secretion of man, and in addition to attack cellulose.

In the Arthrozoic Series the *Insecta* and *Crustacea* possess well-defined alimentary canals, from which the products of digestion are absorbed by the cells lining the walls and received into venous vessels and receptacles which not only serve the purposes of circulation but act also as absorbent agents for the

chyle. This method of conveying the nutriment to the cells marks the *Insecta* and *Crustacea* from the *Invertebrata* already considered, in which the products of digestion transuded directly through the endoderm in the more specialised forms, or originated within the cells themselves in the simpler, and from the *Vertebrata*, in which the absorbent and circulatory vessels are distinct from one another. The members of these orders possess salivary glands secreting an active diastatic ferment, a "liver" or pancreas, the secretion of which acts on starch, proteids, and fats, and can produce amido-acids from proteid bodies.

The *Polyzoa* in the Malacozoic Series revert to the mode of digestion and absorption characteristic of certain of the lower forms, in that their digestive canal though complete is suspended in a somatic cavity into which the products of digestion transude and are absorbed by the lining cells.

In the *Mollusca* the further advance of an acid secretion especially provided in the stomach for the purposes of digestion may be noted as the first indication of a separation in function of that organ from the bowel. As before, the "liver" of the *Mollusca* possesses all the characteristics of a pancreatic gland whose secretion can act on starch, albumin, and fats. Barfurth calls it a hepato-pancreas, but there appears no evidence to show on physiologico-chemical grounds that the gland possesses any of the functions of a true liver.

It has been lately termed the "Mitteldarmdrüse," the mid-gut gland, and, according to Krukenberg, acts as a compound gland with the properties possessed by the salivary, gastric, and pancreatic glands united. He has found that its secretion acts in one instance in an acid solution, in another in an alkaline medium, and again in a neutral fluid with the same power; while in those molluscs in which acid secretions are wanting the secretion of the gland is inert in the presence of acids, and conversely, as in *Helix Pomatia*, its secretion can only act in the presence of acids.

The *Tunicata* present very analogous features.

A study of the arrangements provided for the preparation of food, and the extraction from it of the needful constituents in an assimilable form among the various members of the *Invertebrata*, reveals a regular and progressive advance towards sub-division of function and increase in complexity of the apparatus employed.

The lowest type of digestive power may be ascribed to the purely parasitic forms inhabiting the alimentary tracts of higher

species, and deriving their nourishment from the already digested substances dissolved in the fluids which bathe them. Such forms possess no alimentary canal, no digestive organs, nor do they secrete any active digestive ferments; they absorb all their nourishment through their outer covering. The next stage is represented by those animals which ingest their food either by their external surface or by a rudimentary aperture, but possess no other means of digesting the food thus obtained than the intrinsic action of protoplasm. Though physically much more simple in formation than the preceding class they possess a higher digestive power. Immediately above this class may be placed those animals in which, though possessing some form of alimentary canal, digestion is performed within the cells of the endoderm, and distribution of the products is carried on by simple intracellular diffusion. Further progress is shown by the secretion of a digestive fluid into the alimentary canal, and by the absorption of the products of its action by the cells lining the tract or the somatic cavity. This stage proceeds through many additional stages until the highest type of invertebrate digestion is reached. At first the fluid secreted for digestion is common to the whole tract; little by little separate segments become adapted for special functions; pyloric cæca, attached to the stomach, secreting a pancreatic juice, salivary glands, the so-called liver or pancreatic gland round the intestine, and the differentiation of the alimentary canal itself into definite portions mark these advances. The methods of absorption of the products of digestion and their circulation through the tissues can also be traced from the simplest form to one in which a complex arrangement of organs and vessels is present. In the lowest members of the *Invertebrata* the single cells which constitute their entire bodies require no means for the distribution of the nourishment save the intracellular movements of the sarcode forming them. In slightly higher forms the products of intracellular digestion diffuse through from the active cells to those which do not come into direct contact with the food, as in the compound *Protozoa*, or pass by a similar process from the endodermic cells to the cells of the meso- and ecto-derm as in the *Hydrozoa*, or, as in the *Actinozoa*, transude through the endoderm of the alimentary canal and are absorbed by the cells lining the somatic cavity from which they pass by a process of diffusion throughout the tissues. The nutriment absorbed by

the endodermic cells in the *Annelida* is conveyed to the tissues partly by inbibition and diffusion, partly by means of pseudo-hæmal vessels. The classes following the *Annelida* possess vessels which serve the double function of carrying the blood and of conveying the absorbed nutriment to the cells of the body. There are thus in the *Invertebrata* no absorbent vessels analogous to the lymphatics of the *Vertebrata* and distinct from the vessels carrying the blood, and it is only in the higher forms that such vessels are found.

In tracing the development of the alimentary canal we have found that in forms below the *Actinozoa* it is identical with the body cavity, but that in all the higher forms, save the *Tunicata*, it is distinct from this cavity. As low down as in some of the *Protozoa* a rudimentary œsophagus marks the first appearance of a digestive tube, but it is not until the higher Echinodermata are reached that the alimentary canal shows any trace of a specialised portion corresponding to a stomach. In the *Annelida*, *Arthropoda*, *Polyzoa*, and *Mollusca* a true stomach is present. In the *Insecta* a crop is also provided, and in the *Rotifera*, *Oligochæta*, the higher *Insecta*, *Polyzoa*, *Gasteropoda*, and *Cephalopoda* a gizzard is observed. In connection with the apparatus provided for mastication of the food in addition to the gizzards in the *Echinodermata*, the *Echinidea* possess five hardened epithelial jaws each bearing a tooth. A further advance may be noted in the hardened buccal epithelium in *Lumbricus* and *Hiruda*, forming analogous structures to the teeth of the *Vertebrata*. The *Arthropoda* present more highly-developed structures. In the majority of the species the mouth is furnished with hard crushing jaws, or mandibles, and more delicate maxillæ, while in many these structures are developed into masticatory and prehensile claws. In the *Crustacea* indeed two mandibles, four maxillæ, and three pairs of feet-jaws (*maxillipedes*) are all adapted for the prehension and mastication of food. Various modifications of these structures are met with in the *Insecta*, while the *Mollusca* possess a radula or odontophore which may be regarded as a still further advance in that it seems to combine the properties of both teeth and tongue. Among the numberless members of the numerous classes of the *Invertebrata*, from the microscopic and apparently insensible *Amœba*, the delicate and sensitive *Actinia* or sea-anemone, to the wasp or bee, and to the molluscs, the apparent means of digestion are widely dissimilar, although the results are the

same; the lowest in the scale is as capable of choosing the food suited for its nutrition, and of rejecting the unsuitable, as the highest organism. Whatever be the particular mode by which the food-elements are obtained and absorbed, the great underlying principle consists in the properties of living cell-protoplasm, properties combined in a single cell or specialised in different series of cells, by which it can so alter the chemical attributes of native food substances as to render them assimilable with its own constituents. Those forms which do not require to digest their food, as in the *Cestoidea*, possess no power of digestion; those which do not require more carbon than that supplied in proteids, or obtained from water or air through the agency of pigments akin to chlorophyll, do not possess an amylolytic ferment, nor are they stimulated to exert any of the associated acts accompanying the digestion of carbo-hydrate substances. In others, as for instance in the sponges, where the digestive processes are entirely intracellular, the cell-protoplasm forms a ferment capable of acting on proteids, carbo-hydrates, and fats. The protoplasm of one series of identical cells is thus capable of transforming each of the three elements of the food into the same derivatives as the secretions of specialised groups of cells in the higher animals.

TABLE L.—*The Salivary Glands and Salivary Constituents in the Invertebrata.*

Salivary Glands are present in	Oligochæta.	Orthoptera.	Lepidoptera.	Hymenoptera.	Arachnida.	Gasteropoda.	Cephalopoda.
Diastatic ferment	+	+	+	+	+	+	+
Mucin	?	-	-	-	-	+	+
Sulphocyanates	?	+	+	-	+	+	+
Calcium	?	+	?	-	-	+	+
Reaction	Alkaline.	Alkaline.	Alkaline.	Neutral.	?	Alkaline.	Alkaline.

TABLE LI.—*The Organs capable of Digestion in the Invertebrata.*

	Protozoa.	Porifera.	Cœlenterata.	Echinodermata.	Oligochæta.	Orthoptera.	Lepidoptera.	Hymenoptera.	Arachnida.	Crustacea.	Lamellibranchiata.	Gasteropoda.	Cephalopoda.	Tunicata.
Intracellular	+	+	+	–	–	–	–	–	–	–	–	–	–	–
Unicellular	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Endodermic	–	+	+	–	–	–	–	–	–	–	–	–	–	–
Extracellular	–	–	+	+	+	+	+	+	+	+	+	+	+	+
Salivary glands	–	–	–	–	+	+	+	+	+	+	+	+	+	–
Pancreatic glands—														
Pyloric cæca, or glands	–	–	–	+	–	+	+	+	–	–	–	–	–	–
So-called liver	–	–	–	–	+	–	–	–	+	+	+	+	+	–
Savigny's tubules	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Diastatic ferment—														
Intracellular	–	+	+	–	–	–	–	–	–	–	–	–	–	–
Salivary	–	–	–	–	+	+	+	+	+	+	+	+	+	–
Pancreatic	–	–	–	+	+	+	+	+	+	+	+	+	+	+
Proteolytic ferment—														
Intracellular	+	+	+	–	–	–	–	–	–	–	–	–	–	–
Pancreatic	–	–	–	+	+	+	+	+	+	+	+	+	+	+
Peptic	–	–	–	–	–	–	–	–	–	–	–	+*	–	–
Fat Splitting—														
Intracellular	–	+	+	–	–	–	–	–	–	–	–	–	–	–
Pancreatic	–	–	–	+	?	+	?	?	+	+	+	+	+	+
Fat Emulsifying	–	–	–	+	?	?	?	?	+	+	+	+	+	+

* In *Helix Pomatia* (Barfurth and Levy).

THE VERTEBRATA.

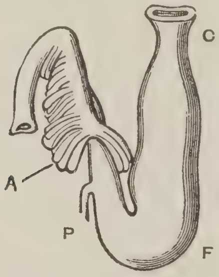
Digestion in Fish.—The lowest class of the *Vertebrata* is formed by *Pisces*. Fish usually possess a complicated dentition, the teeth may not only develop in the jaws but in all the bones entering into the framework of the mouth. The œsophagus opens directly into a large stomach, which is usually furnished with a valve at its lower end. In many fishes a variable number of blind tubes open into the intestine immediately below the pylorus. They are termed the pyloric cæca, and are supposed to represent the pancreas (see Fig. 36). In some fishes, however, a well-developed pancreas is present, while in others the pyloric cæca are wanting. The intestine varies much in length, and in many fish the absorbing surface is increased by

a fold of the mucous membrane winding spirally, screw-like, from the pylorus to the anus. The liver is usually large, and loaded with oil.

The salivary glands are either absent or rudimentary. Krukenberg (*Grundzüge einer vergleichenden Physiologie der Verdauung*, Heidelberg, 1882) found that in the carp the mucous membrane of the mouth secreted a fluid capable of converting starch into sugars. The gastric glands secrete a fluid containing a large amount of pepsin and of acid. It was at one time thought that the pepsin of the fish's stomach differed from that in *Mammalia*, from the fact that it is capable of digesting albumin in an active manner at a temperature of 0° Cent.

FIG. 36.

THE STOMACH OF A SALMON-TROUT.



(Meade Smith, after Carus.)

A, Pyloric appendages; *C*, Cardiac end of stomach; *P*, Pyloric end; *F*, Fundus.

Krukenberg in 1881, and Flaum in 1892, showed, however, that pepsin from the mammalian stomach possessed active properties even at the freezing point if present in large amount.

Richet found that the acidity of the gastric juice in the cartilaginous fishes was 1.5 *per cent.*, while Krukenberg observed that the highest digestive power of the pepsin extracted from the gastric mucous membrane of fish was exercised between the temperatures of 20° and 40° Cent., and with 0.1 to 0.2 gramme of hydrochloric acid per cent., although 1.0, 1.5, and 2.0 grammes per cent. of this acid only slightly retarded its action.

The great activity of the gastric juice of fishes may be gauged by the result obtained by Richet, who was able to complete the peptonisation of

30 grammes of dry albumin by the action of 0.2 gramme of the dried mucous membrane of a fish's stomach, or 1 to 150 parts.

The same observer found that neither 2.3 per cent. of hydrochloric acid, ether and chloroform in excess, nor cyanide of potassium, prevented active digestion.

When first secreted the gastric juice is of a semi-gelatinous consistence, but soon, by a sort of self-digestion, becomes more fluid. In the majority of fishes it possesses no diastatic properties, but in purely herbivorous types, such for instance as the carp and tench, it has been found to act on starch.

It has been suggested with the view of explaining the rapidity with which carnivorous fish digest their food, and the short time which elapses between the entrance of large masses into the stomach and their disappearance from it, that gastric proteolysis in fishes is largely due to bacterial action. Some have gone so far as to assert that bacteria are the sole agents in the gastric digestion of fishes. A suggestion such as this, put forward to account for the celerity of digestion, is manifestly at fault, because the most rapid proteolytic action caused by micro-organisms is never complete in so short a time, while the gastric juice is much above the acidity required to inhibit or arrest bacterial growth. The high acidity and the large proportion of pepsin in the secretion of the gastric glands is quite sufficient to account for the rapidity of digestion in fishes, a rapidity which possibly appears to be greater than in reality, owing to the habit many fish have of ejecting the contents of the stomach directly they are sensible of anything tending to fetter or confine their movements. Indeed, vomiting forms the normal way by which carnivorous fish get rid of any bulky indigestible matter swallowed. There is no doubt that the œsophagus and stomach of fishes often swarm with bacteria; the stomach, however, contains few organisms while active digestion is going on, and these are chiefly non-motile forms which do not liquefy gelatin and are incapable of peptonising albumin to any extent. Between the periods of gastric activity the contents of the stomach are very slightly acid (Richet), mucoid in character, and offer no hindrance to organismal growth.

The digestive processes in the salmon, *Salmo Salar*, are of peculiar interest owing to the mystery which has long enveloped the life-history of this remarkable fish, and which indeed has even now been only partially cleared up. All the

best authorities concur in believing that the salmon does not feed in fresh water. His in 1873, and Barfurth in 1875, came to this conclusion from the practical examination of the intestinal tract; while Miescher-Ruesch in 1880 published a voluminous report on the life-history of the salmon in the Rhine, and stated categorically that "the Rhine salmon takes no food from the time when it quits the sea until it spawns, and as a rule not even after that" as long as it remains in fresh water. He found also that the mucus in the stomach and bowel is never of acid reaction, and that the glycerine extracts of the mucous membranes of these organs only exert a feeble digestive action in artificial experiments on fibrin in the presence of hydrochloric acid. He concludes that no active digestive secretions are formed by the salmon in fresh water. The writer can corroborate this statement. During a course of experiments undertaken for the Scottish Fishery Board in 1895-97 glycerine extracts made from the gastric mucous membrane of salmon caught either in tidal waters or at the heads of fresh-water streams were capable of converting not more than one-third of raw egg-albumin into peptone, compared with a proportion of over 90 per cent. digested by pepsin under the same conditions—*i.e.*, digestion at the ordinary temperature for twelve hours. Of the thirty-two salmon tested only fourteen exhibited so great a peptic power, the average quantity of albumin acted on by the total number being as low as 11.1 per cent. The fish caught in the higher reaches afforded a glycerine extract of higher proteolytic power than those caught at the mouth, owing to the peptic activity in kelts. On an average the extract of the stomach mucous membrane of the fish caught at the mouths of the rivers was capable of acting on 9.5 per cent. of albumin, from the fish caught higher up the rivers on 10.37 per cent., and from the kelts on 22.7 per cent. of the albumin. If the figures obtained for the kelts are subtracted, the upper fish possessed rather less peptic power than the fish from the estuaries. Coincident with this failure in proteolytic power the glands of the gastric mucous membrane were found to be atrophied. And it is interesting to find that in the kelts the glands were beginning to re-form when the gastric extract was found to be more active. The objections which may be urged against the statement that salmon do not feed in fresh water consist in the fact that they rise to the fly, and the fact that the ovary

and testis, while only forming about 3 per cent. of the body-weight before the fish enter the rivers, reach to as much as 15 per cent. in the case of the ovary, or 8 per cent. in the testis, of the total weight of the fish. How can such an increase in these organs be accounted for if the salmon do not take food? Careful analyses of the flesh and "curd" of salmon during the various stages of their ascent of the rivers have shown that the loss in nitrogen and in fat in them is more than sufficient to account for the whole of the increase of the ovary or testis. This fact is one of the greatest importance and significance in connection with general metabolism. The transference of elements from one tissue to another in such quantity that an organ can increase about four thousand-fold, while at the same time the necessary amount of these elements are being consumed in the production of muscular energy and for the preservation of vital processes, constitutes one of the most remarkable facts known to us.

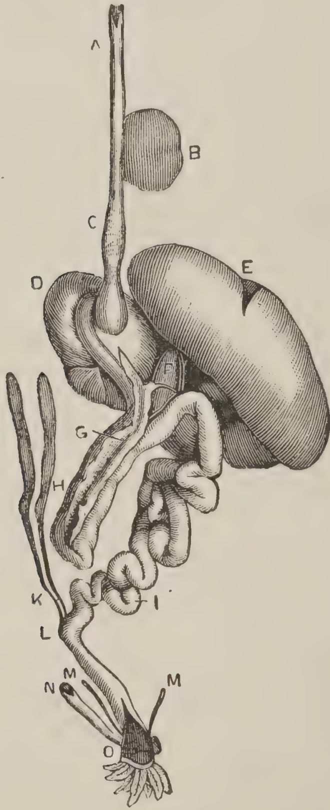
Cultivations of the organisms present in the alimentary canal of the salmon at different periods of the year and from different parts of the streams show (see Chart X.) that as the year advances and the water becomes warmer a greater number of colonies can be grown from the canal. Curiously enough, the figures for May and June, relating to fish caught in Scotland, remain very low, the great annual rise not taking place until July and August. In cold weather the colonies grown from the stomach and intestine tend to exceed those cultivated from the œsophagus, while in warm weather the contrary is found to be present. The upper-water fish contain a larger number than the fish from tidal waters, and the difference is most marked in the case of putrefactive bacteria.

Digestion in Birds.—The influence of the mode of nutrition and the nature of the diet on the structure and development of the intestinal canal is nowhere so marked as in the *Aves*. The members of this division may be divided into the frugivorous, or graminivorous, and the carnivorous classes. The intestinal canal is of greater length and complexity in birds living on fruits or seeds. In all there is a well-marked œsophagus corresponding in length to that of the neck, and in width and elasticity to the nature of the food (see Fig. 37). The œsophagus is often provided, especially among graminivorous birds, with a dilated portion or diverticulum forming the *ingluvies* or crop. In birds

living upon fruits and insects this diverticulum is absent. The goose, swan, turkey, ostrich, and many of the waders possess large crops; the pigeon has two, one on each side of the œsophagus. Some of the carnivorous birds, such as the

FIG. 37.

THE ALIMENTARY CANALS AND ASSOCIATED GLANDS IN BIRDS.



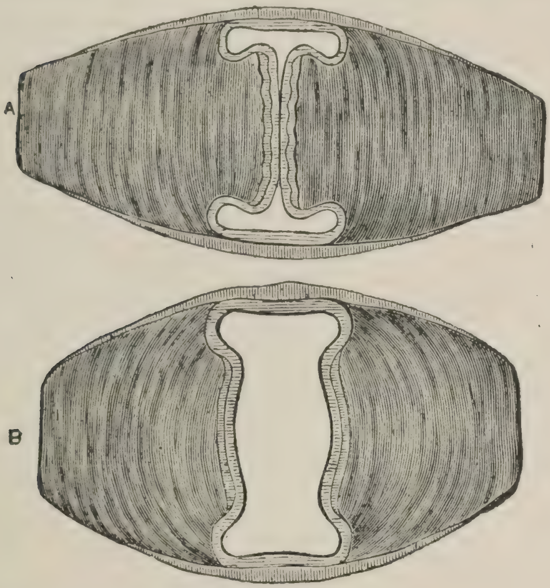
(Meade Smith.)

A, Œsophagus; *B*, Crop; *C*, Infundibulum; *D*, Gizzard; *E*, Liver; *F*, Gall-bladder; *G*, Pancreas; *H*, Duodenum; *I*, Small intestine; *K*, Cæca; *L*, Large intestine; *M*, Ureters; *N*, Oviduct; *O*, Cloaca.

pelican, possess a similar dilatation of the gullet, but in them it is placed much higher up, generally below the lower jaw, constituting rather a reservoir or pocket for the storage of food than a true *ingluvies.* The crop of birds acts much in the same way as the rumen in *Ruminantia*, allowing the food retained in it to become macerated amid the juices present (cf. p. 266).

FIG. 38.

GIZZARD OF GOOSE (HORIZONTAL SECTION).



(Meade Smith, after Jarrod.)

A, Contracted; *B*, Relaxed.

Note that the contraction of walls in *A* apposes only those parts where the horny walls are especially thick, leaving spaces at the edges for fluids and finely crushed foods to accumulate.

The œsophagus narrows below the crop and then expands into a small, dilatable stomach or *proventriculus*, which is furnished with a glandular layer secreting an acid peptic juice. The proventriculus, or *ventriculus succenturiatus*, constitutes the true stomach in birds. It varies in size and shape in different species.

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The proventriculus opens into the *ventriculus bulbosus*, or gizzard (see Fig. 38). The gizzard is a flattened, ovoid organ, furnished with strong muscular walls and a horny firm layer on its internal surface which answers in function to a *radula*. In many of the carnivorous species, such as the *Raptores*, the gizzard is only slightly developed, and may be represented by a membranous pyloric portion of the stomach, similar in structure and function to the membranous portion of the cardiac end of the equine stomach. The gizzard opens into the duodenum, which is succeeded by the other parts of the bowel in the ordinary way. The small intestine, however, is not so well marked off from the large as in mammals. The length of the canal varies with the food. In birds of prey it is only twice as long as the body, except in the osprey, in which it is eight times that length. In graminivorous birds it is much longer. As a rule the alimentary tract in birds is shorter in proportion to the length of body than in *Mammalia*, but longer than in *Reptilia*. In birds the stomach occupies a position corresponding with the long axis of the body, as indeed is the case in all the lower animals already discussed. In *Mammalia* the position becomes transverse.

As birds are not furnished with the necessary apparatus for mastication of food, they require other means for its trituration. In course of time, therefore, we find that the *Aves*, or at least those members of this division which feed upon vegetable stuffs, have acquired possession of a crop to macerate their food in, and a gizzard in which to bruise the portions so indigestible as to have passed through the stomach in a solid form.

When a graminivorous bird, a pigeon for instance, swallows some corn, the grains pass down into the crop, and remain there, immersed in an acid fluid, for many, it may be for twelve or thirteen, hours. The acid secretion of the crop is poured out in considerable quantities; Spallanzani obtained an ounce of fluid in one hour from the crop of a pigeon, but its specific properties have not been thoroughly studied, nor is it known whether it contains any ferment or not. Unbroken grains and seeds do not seem to be appreciably softened even after a stay of twelve hours in the crop, but there is probably some diastatic action brought about in it during that time on unprotected starch granules.

The unbroken grains passing from the crop into the proventriculus cannot be acted upon by the gastric juice, as this secretion is incapable of dissolving their coating of cellulose. (The gastric juice contains hydrochloric acid, pepsin, and a milk-curdling ferment.) The grains then pass into the gizzard, where they are comminuted between the muscular walls and small stones and pebbles swallowed by the bird, while the gastric juice secreted by the proventriculus, flowing down into the gizzard, acts readily upon the proteids exposed by the breaking up of the grain envelopes. John Hunter observed and noted in 1792 that the crop of the pigeon, and probably of other birds, undergoes a change during the time of incubation, and for some time afterwards. Both sexes show the change, which consists in a thickening of the mucous membrane with an increase in its vascularity, and the pouring out of a milky fluid from the open mouths of the glands. This fluid, it is asserted, is regurgitated and used for the nourishment of the young birds during the first days of their life.

In birds, therefore, the absence of a means of masticating the food is compensated by the presence of hollow organs for its maceration, and by the possession of a muscular gizzard adapted for bruising the solid matters contained in it.

Digestion in the Reptilia.—The alimentary canal in the amphibious reptiles closely resembles that in fishes. The œsophagus is short, dilatable, and muscular, the stomach tubular, and the junction of the small with the large intestine is well marked. The influence of the nature of the food on the development of the canal is well illustrated in the frog. During the tadpole stage the animal is herbivorous, and possesses a long, coiled intestine; but on reaching its full development the frog becomes insectivorous, has no need for so long an intestinal canal, and therefore is provided with one relatively much shorter.

The crocodile forms a connecting link between the reptiles and the birds, with a strong muscular stomach not very unlike the avian gizzard. In it also the first differentiation of the duodenum from the rest of the small intestine appears, with hepatic and pancreatic ducts emptying into it. It is as well the lowest animal in the scale provided with a true mesentery. In *Ophidia* the cardiac portion of the stomach is long and dilatable, the pyloric end narrow and muscular. In

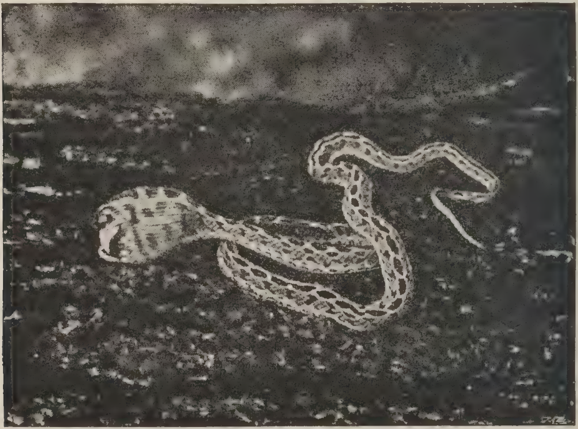
DASYPELTIS SCABRA SWALLOWING EGG.

FIG. 39.

Photo, R. F. Nesbit.] [*Copyright.*

Skin so stretched that distinct apertures are formed between bones of lower jaw. Muscles of jaw not yet so stretched that the jaw-bones are separated at the hinge or socket.

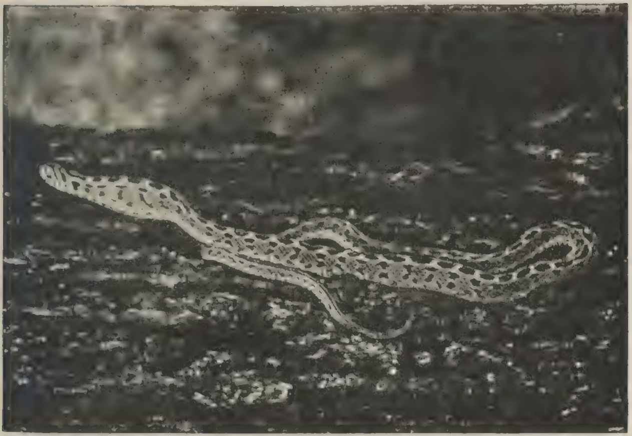
FIG. 40.



Photo, R. F. Nesbit.] [*Copyright.*

Egg fairly in jaws. Tension now so great that jaw-bones are forced out of socket, a wide expanse of skin and ligament separating them.

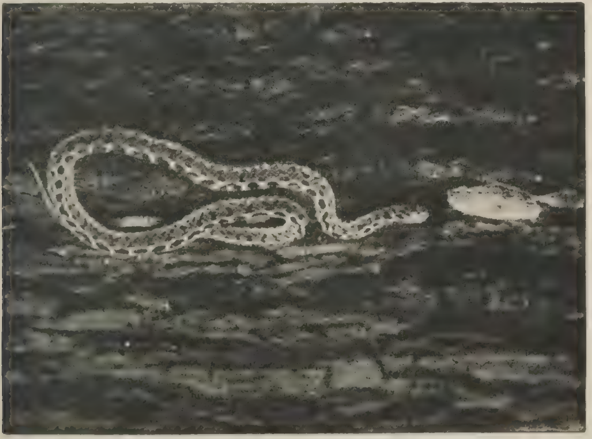
FIG. 41.



Photo, R. F. Nesbit.] [*Copyright.*

The under sides of vertebræ almost immediately behind head are elongated, forming a row of nine or ten saw-like teeth. These project through the membrane of the œsophagus and are used to crack the shell longitudinally. A powerful contraction of muscles of neck then causes the shell to collapse.

FIG. 42.



Photo, R. F. Nesbit.] [*Copyright.*

Ejection of the whole of the shell, held together by the skin of the egg, in the shape of a pellet.

the carnivorous reptiles the intestines are short and sacculated; in the herbivorous members of the order, long and provided with cæca.

The mechanism of the jaws and teeth of snakes is one of considerable interest. The palatine bones never unite directly with the vomer, but are usually connected with the maxillæ by short bones placed transversely, and by the pterygoids with freely movable quadrate bones. Thus the connection of the bones of the jaws with the other bones of the skull is rendered lax, and permits in some species a very marked range of movement. The two mandibles of the lower jaw are only joined together at the symphysis in front by elastic fibrous tissue.

Owing to the loose connections of the bones the rami of the mandibles can be separated widely from one another, while "the squamosal and quadrate bones constitute a kind of jointed lever, the straightening of which permits of the separation of the mandibles from the base of the skull" (Huxley). The possibility of such free movements of the bones explains the ease with which a snake can swallow objects much greater in diameter than that of the mouth or throat in a passive condition.

In *Crotalus*, the rattle-snake, as in other poisonous forms, the upper maxillæ form elongated hollow fangs, inclined backwards and downwards when the mouth is shut, but assuming a vertical position when the mouth is widely opened. When a snake strikes, contraction of a muscle which extends over the poison-gland at the base of the maxilla forces some of its contents through the hollow canal into the wound made by the fang. The ordinary teeth in snakes, apart from the fangs of the poisonous varieties, are usually curved backwards to aid in the retention of the prey.

In *Rachiodon*, the egg-eating African variety, the teeth are poorly developed and rudimentary, but the inferior spinal processes of the first eight or nine vertebræ are long, tipped with dense enamel, project into the cavity of the gullet through its dorsal wall, and serve to break the shells of the eggs, which are swallowed whole and remain unbroken until they reach a portion of the alimentary canal from which none of their nutritious contents can escape. The fragments of the shell are rejected through the mouth shortly after the contents have been removed (see Figs. 39-42).

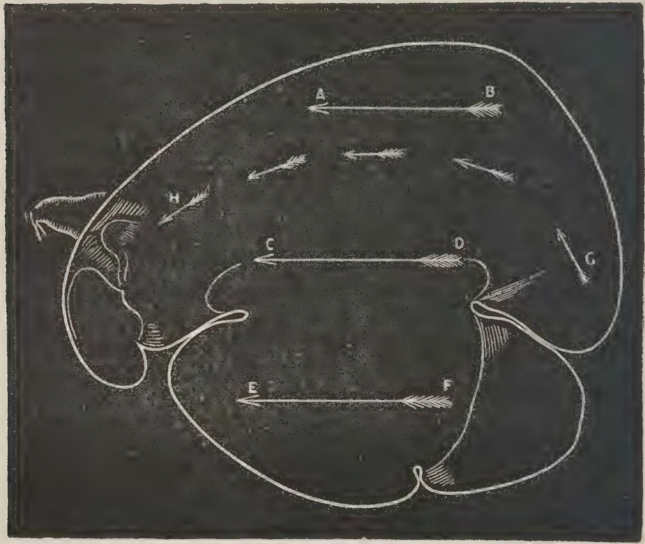
Rumination.—In the carnivora and omnivora the food reaches the stomach in a sufficiently divided state to be at once acted on by the gastric juice. In some birds and crustaceans, as we have seen, mastication in the mouth does not occur, but the food is crushed and comminuted in an accessory stomach or gizzard. A third type is seen among the ruminantia. As a large quantity of their food is required to yield the necessary amounts of nutritious elements, time is saved by its rapid passage through the mouth and gullet in an imperfectly chewed state, to be regurgitated at leisure in a form which can be much more easily manipulated. In the wild state, ruminant animals require to be able to obtain their food rapidly. Relying on acute powers of sight, hearing, and smell, and rapid movements to escape from their foes, they can in a short time obtain a supply of food stored up in their œsophageal pouches, and then retire to some safe retreat to masticate and digest it.

The grass brought by the prehensile tongue between the lower incisor teeth and the hard pad over the upper jaw is quickly severed, slightly bruised by a few movements of the molar teeth, and passed down the gullet. When solid food is swallowed, it enters the rumen or paunch, an enormous dilatation of the œsophageal canal, or, passing on, reaches the reticulum, the waterbag, or honeycomb stomach, which communicates with the rumen by a wide opening (see Figs. 43 and 44). The food is constantly driven back and forwards before regurgitation from the one cavity to the other by peristaltic action of the walls. These two portions of the stomach are looked upon as belonging to the cardiac end of the stomach proper by some authorities, or as dilatations of the œsophagus by others. The arrangement of the epithelial cells lining both cavities is more suggestive of the correctness of the latter view. The cells are arranged in rows somewhat like the cells of the skin epidermis, and here and there the surface is elevated in the form of papillæ. In the reticulum the mucous membrane is raised into folds which cross each other at an angle, enclosing hexagonal depressions, whence its name "honeycomb" stomach arises. The rumen constitutes much the largest of the four stomachs of the ruminant, representing nine-tenths of the total space, while the reticulum is the smallest of the cavities. The reticulum communicates by a narrow orifice with the third stomach, the psalter, omasum, or manyplies. The psalter

is placed on the right side of the rumen and reticulum, and is lined with mucous membrane, disposed in voluminous folds of various heights, but most of them capable of extending completely from side to side across the cavity. The third stomach is thus formed into a bag containing numerous narrow channels between folds of the mucous membrane, and acts

FIG. 43.

VERTICAL SECTION OF THE RUMEN AND RETICULUM OF THE OX.



(Meade Smith, after Colin.)

AB, Superior region; *CD*, Median region; *EF*, Inferior region; *GH* show the direction taken by the food passing from the posterior part of the rumen to the œsophagus before the act of rumination.

as a strainer in preventing coarsely comminuted food from passing on to the fourth stomach. The opening of the œsophagus is situated at the junction of the rumen and reticulum, and is guarded by muscular folds, which stretch longitudinally from the entrance to the psalter along the roof of the reticulum. When the free edges of these folds are approximated, a groove is formed leading directly from the

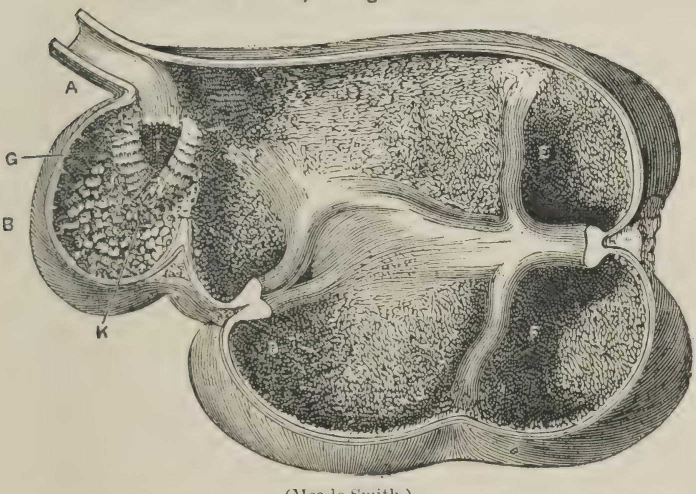
œsophagus to the third cavity or psalter. In none of these portions of the stomach are there any glands capable of secreting an active digestive fluid. In the rumen a few mucous glands are present, but the psalter is entirely destitute of any glandular structures.

The fourth stomach, the abomasum or rennet, is the only one which corresponds in histological structure to the stomach of other mammals. It is slender and elongated, with a mucous

FIG. 44.

THE RUMEN AND RETICULUM OF THE OX.

The left wall is seen, the right has been removed.



(Meade Smith.)

A, Gullet; *B*, Reticulum; *C*, *D*, *E*, and *F*, the anterior, middle, postero-superior, and postero-inferior pouches of the rumen respectively; *GK*, Œsophageal pillars; *I*, Exit leading into manyplies or omasum.

membrane raised in one or two longitudinal folds, and studded with gastric glands. It is in this division of the stomach that the processes of true digestion occur.

When a ruminant drinks, the water enters the rumen and reticulum, and in part is carried into the psalter by the œsophageal groove, and from thence into the fourth stomach. The portion which enters the rumen and reticulum soon finds its way through the third into the fourth cavity. In the calf, the

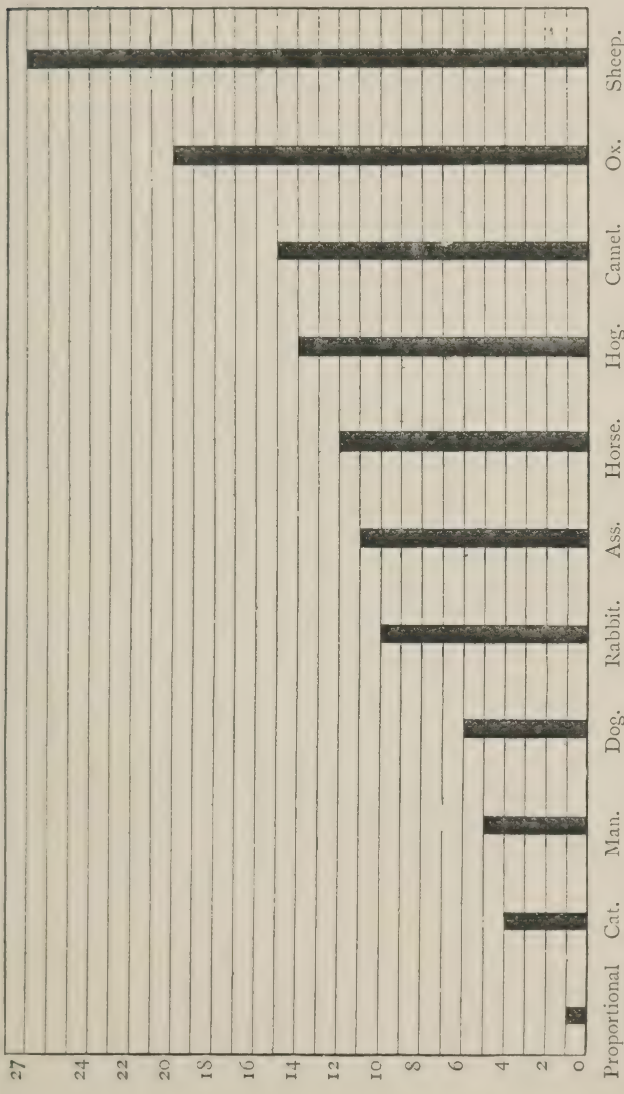
milk is conveyed into the true digestive portion of the stomach, or abomasum, by the same means.

The amount of fluid conveyed directly into the second stomach by the œsophageal groove or gutter is small, owing to the oblique angle which the gutter forms with the gullet. When coarsely-ground solids are introduced into the paunch and reticulum their further passage into the abomasum is rendered impossible by the close meshwork of the folds in the manyplies. Solid food thus remains in the rumen and reticulum, where it is subjected to the action of the liquids contained in them—the swallowed saliva, mucus, and water. The rumen and reticulum appear always to contain food. Colin found up to two hundred pounds, three-fourths of which consisted of water, in the rumen of an ox which had fasted for twenty-four hours. In these organs the food is macerated for hours together, the length of its stay being proportionate to its digestibility. The reaction of the fluids in the first two stomachs in adult animals is alkaline; Gmelin and Tiedemann, however, found an acid reaction on testing the contents in calves, and it appears that the fluids contained by the rumen and reticulum may become acid if the processes of normal digestion are disturbed. (Diagram I.)

The food during its stay in the first portions of the stomach is subjected to a constant churning movement, and is thereby mixed with the remnants of the food previously taken in, which have not been passed on after a second mastication into the true gastric cavity.

We have seen that the mucous membrane lining the rumen and reticulum are devoid of glands capable of secreting an active digestive fluid. There may be some secretion of an alkaline fluid from the scanty glands which are present, but the chief source of the alkali found in the contents is ascribed to the swallowed saliva. Prolonged treatment with an alkaline fluid containing a diastatic ferment at the body temperature forms the best possible means for the conversion of starches into maltose or soluble dextrins, and thus the grass or leaves eaten by a ruminant are not only churned up into a pulpy mass before regurgitation, but are also so far acted on that most of the accessible starch is converted into simpler derivatives. In addition to this diastatic action some fermentative processes are certainly present in these organs, though what end they serve is obscure. A temperature of 40° C. and a slightly

DIAGRAM I.—Showing the Relative Proportion between the Length of the Body and of the Alimentary Canal in Mammals. (Length of Body = 1.)



If the length of the body in each case be taken as one (first column on the left), the height of each column represents the length of the Alimentary Canal in the different animals as compared with it.

alkaline medium afford the best possible nidus for the growth of bacteria, yeasts and moulds, while carbonic acid and sulphuretted hydrogen gases, acetic acid, butyric acid and salts, such as carbonates, chlorides, and phosphates, are constantly found in the contents, demonstrating the presence of fermentations of which one or other of them may be the product.

When a ruminant such as one of the domestic animals has eaten its fill, in time, urged by a sense of repletion, it lies down, reclining slightly to one side, and resting less on the abdomen than on the thorax. Its fore-legs are usually flexed beneath the chest, the hind-legs stretched forward and placed under the abdomen. To allow of rumination taking place, the rumen must be distended with food to an extent sufficient to allow contractions of the diaphragm and abdominal muscles pressing upon its walls, but must not be too full, lest the walls of the rumen be paralysed. As no true digestion takes place in the first three stomachs, a ruminant whose rumen and reticulum are nearly full of food, but not in a sufficiently distended state to allow the action of the abdominal muscles to take effect, may die of hunger if deprived of further nourishment. All ruminants require an abundance of water. They especially seek it immediately before rumination, for a reason which must be very patent—to fill the rumen and render the contents more fluid. The camel at first sight would seem to be an exception to the rule that all ruminants must have a good supply of water, but in this animal, as in the llama and other members of the *Ruminantia* inhabiting desert places, the reticulum and the rumen possess numbers of depressions or cells in their walls, the mouths of which are supplied with muscular sphincters capable of tightly closing the orifices. In the camel and dromedary there are about eight hundred of these cells arranged in two groups, one on each side of the fleshy prolongation of the single œsophageal pillar present. These cells generally contain water, and are regarded as reservoirs adapted for this purpose. The cells in the camel are capable of holding about ten quarts (see Fig. 45).

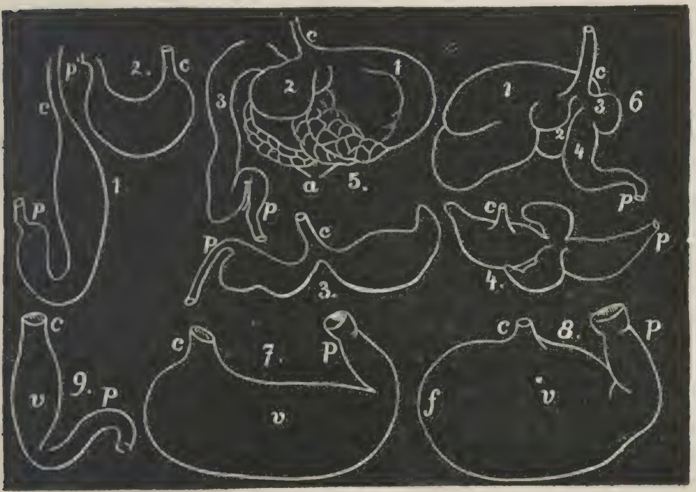
When the rumen is sufficiently full to initiate rumination the animal ceases feeding and generally lies down in the comfortable attitude described. As the cud is being gently churned about in the rumen part of it will push against the pillars of the œsophageal opening. The impulse thus produced appears to act as a stimulus to the diaphragm and abdominal muscles,

causing their contraction and the forcing of some of the contents into the lower portion of the œsophageal tube, from whence reverse peristalsis conveys it up to the mouth.

Some authorities look upon the reticulum as the active part of the stomach in this process, others believe that the bolus passes directly from the rumen. It seems to be more probable that the reticulum has much to do with it. It is smaller, has more muscular walls, and communicates more directly with the gullet. But the reticulum is not indispensable for the regurgitation of food. Flourens sewed up the reticulum in a sheep and rumination still continued. Colin showed that the mere introduction of food between the pillars of the œsophagus caused an act of regurgitation.

FIG. 45.

OUTLINES OF THE STOMACHS OF VARIOUS MAMMALS AND OF A TURTLE.



(Meade Smith, after Thanhoreff.)

Stomach of
1. Seal.
2. Hyena.
3. Cricetus.
4. Manatee.
5. Camel.
6. Sheep.
7. Lion.
8. Horse.
9. Turtle.

c. Cardiac end.
p. Pyloric end.
v. Ventriculus.
f. Fundus.

1, 2, 3, 4 in small type indicate the first to fourth stomachs in animals with compound gastric organs.

From whichever cavity the regurgitated bolus is derived, the essential factors in the process of rumination are the slow movements of the stomach walls and the contractions of the diaphragm and abdominal muscles. Should the diaphragm be paralysed, as by section of the phrenic nerves, the abdominal muscles can exercise the requisite pressure by increased action, but if the pneumogastric nerves are also divided no act of rumination can take place. As the muscular contractions accompanying the act take place, visible movements may be observed in the flanks of the animal. These movements are akin to the movements of ordinary respiration but are more marked. An inspiratory effort is rapidly followed by expiration. This is coincident with the engagement of the bolus in the gullet, and only becomes energetic in character if the contents of the rumen are drier than is natural. The contractions of the abdominal muscles exert pressure on the gastric organs, while the diaphragm during contraction serves to enlarge the thoracic cavity and thus to partially aspirate or suck the cud upwards. On arrival in the mouth the surplus water of the cud is swallowed again and the solid part conveyed by the tongue between the cheeks and the molar teeth. About one hundred or one hundred and twenty grammes usually constitute each bolus. If an ox be fed on twelve kilogrammes of hay in the day, a food which absorbs four times its weight of water in the mouth and rumen, the resulting sixty kilogrammes will require five to six hundred individual acts of rumination to take place before all of it can be masticated a second time. As each act lasts about fifty seconds, seven hours out of the twenty-four will be occupied in rumination if all the food be thus dealt with. Even if some of it escapes regurgitation the total duration of rumination in the ox can hardly be less than six hours out of the twenty-four, or a fourth part of the day. Ruminants cannot therefore be employed for constant work and still perform the processes necessary for the complete digestion of their food and for the preservation of their health.

Rumination presents the appearance at first sight of being a voluntary process. It seems to occur only when the animal is disposed to commence to chew the cud. It is in addition easily arrested by nervous agencies. Fright, separation of the cow from the calf, and over-exertion tend to stop the process. It is, nevertheless, reflex in origin, the necessary stimulus

arising from the terminations of the sensory nerves in the rumen and reticulum. Section of the vagi, by destroying the centripetal path to the brain, arrests it. Luchsinger was able to produce the essential movements of rumination in animals deeply under the influence of morphine by local stimulation of the rumen, while he found that the movements of the jaws and the secretion of saliva from the parotid gland could be produced by such stimulation even when division of the œsophagus had rendered the return of the bolus into the mouth impossible.

The position of the controlling nerve-centre is placed in the medulla, probably close to the true vomiting centre, and, indeed, rumination may be regarded as a modification of vomiting in which only a certain amount of the stomach contents is regurgitated, no escape of the matter returned occurs from the mouth, and in which the lower opening of the gullet remains firmly closed until the bolus has been thoroughly masticated and again propelled down into the stomach. The food after this second mastication reaches the rumen in a finely divided state and is thus able to pass through the narrow orifice leading from the reticulum into the third chamber, and, through the meshwork of folds encountered in the manyplies, into the true stomach.

In *Ruminantia* the capacity of the stomach is very large (see Diagrams I.–III.). The stomach of the ox can hold as many as from 215 to 290 litres of fluid; of the sheep, 29.6 litres; forming, in fact, 70 per cent. of the total capacity of the alimentary canal in the ox, and about 66 per cent. in the sheep. That is to say that the stomach in these animals is of greater importance for the digestion of their food than the intestine. After the completion of rumination and digestion in the fourth stomach little work remains for either the small or the large intestine.

Digestion in the Herbivora other than Ruminantia.—In those members of this family who do not regurgitate their food the teeth are better adapted for rapid trituration of fodder in order to complete its mastication, while the complicated arrangement of the ruminant stomach is replaced by a simple cavity. The œsophagus in the horse is of small calibre, and boluses of the food swallowed require to be of small size. The stomach (see Fig. 46) of the horse can only contain 15 to 18 litres, while one-half its daily ration may be represented by 5 kilogrammes of hay, which when impregnated with 20 litres of

saliva corresponds to 28 or 30 cubic decimeters. As mastication in the *Solipedes* is slow, two hours will be required for the proper comminution of 5 kilogrammes of hay, and the stomach will therefore be filled and emptied two or three times during this time. A residue of former meals remains in the stomach

FIG. 46.
THE STOMACH OF THE HORSE.

(Meade Smith, after Colin.)

A. Cardiac end. *B.* Pylorus. *C.* Œsophagus. *D.* Duodenum.

until the next is taken. The action of ptyalin on starch continues in the stomach notwithstanding the acidity of the contents.

Owing to the rapid passage of part of the food through the pylorus when the meal is greater in volume than the capacity of

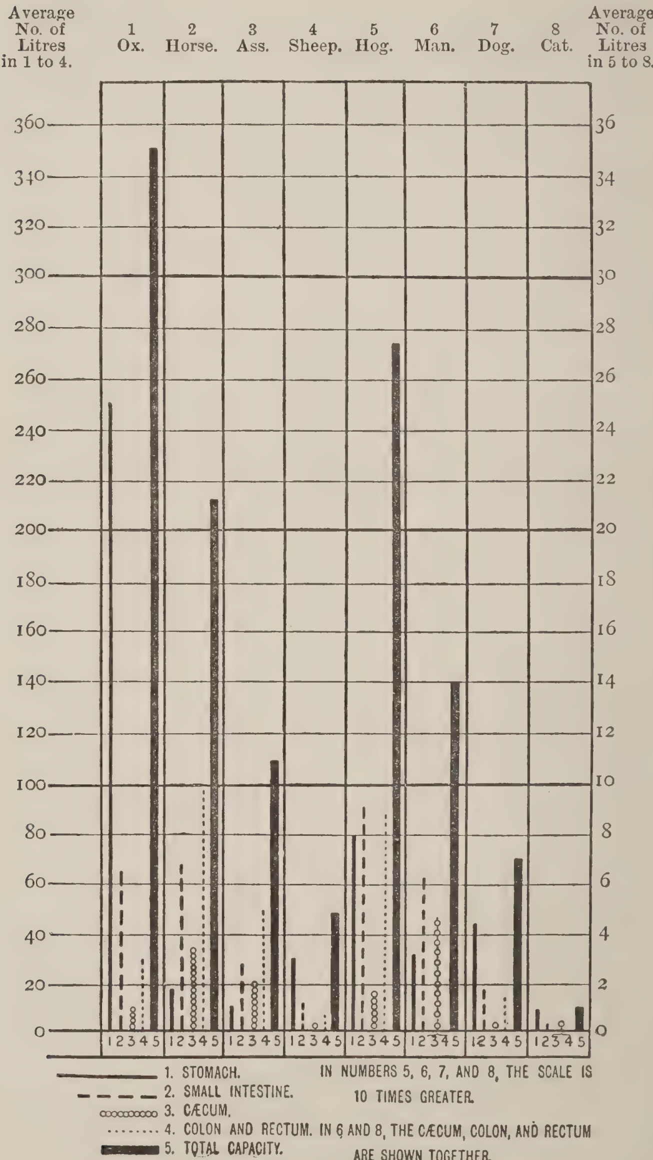
the stomach, it is of importance to give to horses foods which contain the greatest proportion of proteid and carbo-hydrate substances after the lighter foods. Oats should always succeed hay, and water before either. The rapid passage of much of the food through the stomach of the horse necessitates some provision for a more thorough digestion in the intestines than is requisite in the *Ruminantia* or *Carnivora*. For this reason we find that the cæcum and large intestine of the horse (see Diagrams II. and III.) are immensely developed. The cæcum forms a large sac whose length may be greater than that of the body, and with a capacity two or three times that of the stomach. In this part of the alimentary canal the food collects and undergoes a very similar process of fermentation to that already described as taking place in the rumen of the ox.

Vomiting.—In many of the carnivorous birds, in fishes, amphibians, and reptiles, vomiting may be regarded in the light of a normal process. Many birds can eject the contents of their crop with great ease, the matter so ejected in some of the non-carnivorous species being made use of for the nourishment of their young.

Among the *Mammalia* the act of vomiting is pathological, and denotes the presence of a local irritant in the stomach, or of a general irritant in the circulating fluids of the body, capable of acting on the central nervous mechanism involved in vomiting.

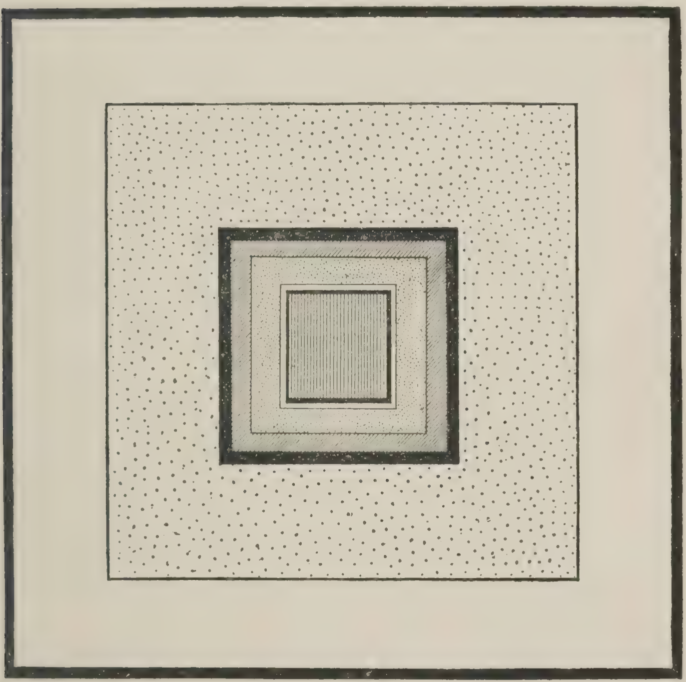
Frogs frequently expel the indigestible remnants of their food from the stomach during the summer months. As the season advances, this process becomes less common, while during winter, when they are hibernating, it ceases altogether. Similarly, the *Ophidia* reject the indigestible portions of their food by vomiting. The carnivorous and omnivorous mammals vomit with great readiness, except in the case of the pig. The herbivorous mammals with a single stomach vomit very rarely and with great difficulty. In fact, the ease with which the contents of the stomach can be expelled by the violent contractions of the muscles of the abdomen and of the gastric walls varies in all animals with the mode of insertion of the œsophagus into the cardiac end of the stomach. In the dog the process is rendered easy by the distance of the cardiac orifice from the pylorus and by the elasticity of the œsophageal walls, which are also expanded into an imfundibular dilatation at the junction with the stomach. Man vomits with greater difficulty,

DIAGRAM II.—Showing the Absolute and Relative Capacity of the Stomach and Intestine of Man and the Domestic Animals.



owing to the smaller size and slight extensibility of the cardiac end of the œsophagus. The horse possesses an œsophagus with thick walls, and a narrow cardiac orifice, usually kept closed by the contraction of a powerful sphincter, and situated in close

DIAGRAM III.—Illustrating the Proportions between the Surface Areas of the Body and Alimentary Canal in Different Animals.



The outer white square represents the Relative Superficies of the Alimentary Canal in the Ox (2.97 : 1) to that of the Body, which is represented by the obliquely shaded square with thick margin, and which is used as the Relative Superficies of the Body in each case.
The outer dotted square represents the same in the Horse (2.18 : 1).
The inner ,, ,, ,, Man (0.79 : 1).
The inner white square ,, ,, the Dog (0.59 : 1).
The perpendicularly shaded square represents the same in the Cat (0.58: 1).

apposition to the pylorus. The pylorus of the horse is of a considerable diameter, and usually remains patent, so that pressure applied to the stomach tends rather to force the contents down into the bowel than up through the œsophagus. Although it is generally stated that many of the herbivora, and notably the horse, are unable to vomit, this is not really the case. All the necessary actions which accompany emesis occur, and part of the food is forced some way up the gullet. The greater part, however, is propelled into the duodenum, and the irritating cause may be so far removed before any portion reaches the mouth that the muscular contractions cease, the upward progress of the food in the œsophagus is arrested and it returns again into the stomach. Ruminants are quite unable to vomit the contents of their true stomach, and can only with difficulty reject the food in the rumen and retriculum even after the administration of powerful emetics; as in rumination, the vomited food is often swallowed again without escaping from the mouth.

Digestive-leucocytosis.—That the number of the white corpuscles or leucocytes of the blood increases after a meal is generally conceded. In man, however, many of the observations as to this increase have proved negative in result, owing to the fact that, given a subject in good health and well-fed with frequent large meals, no good evidence of its occurrence can be detected. If such an individual abstain from food for some hours and then consume a hearty meal, an increase of leucocytes in the blood may be undoubtedly observed. Children, as Reinert and Rieder have shown, exhibit a greater degree of digestive hyper-leucocytosis than adults.

Schiff (*Zeitschrift f. Heilkunde*, Bd. 11, p. 30) counted 19,600 white corpuscles per cubic millimetre in the blood of an infant, born at 4 P.M., drawn off an hour after; at 8 P.M., an hour after the ingestion of 10 grammes of milk, the white corpuscles had increased to 27,625 per cubic millimetre. On the morning of the following day, the infant having partaken of nourishment several times during the night, the number reached 36,000, although the number of red corpuscles had fallen considerably. Luciani enumerated the white corpuscles in the blood of Succi the "fasting man," and found a decrease of their number during the first seven days of fasting from 14,530 to 861 per cubic millimetre. On and after the eighth day the number rose to 1530, and remained steady at that figure up to the end of the thirty days' fast. The health of the individual affects the increase of digestive leucocytosis. Thus Limbeck only found a rise from 12,000 to 14,000 leucocytes in the blood of a well-nourished student after food, but an increase from 3000 to 5400 per cubic millimetre in a thin and half-starved beggar woman. (Charts XII. and XIII.)

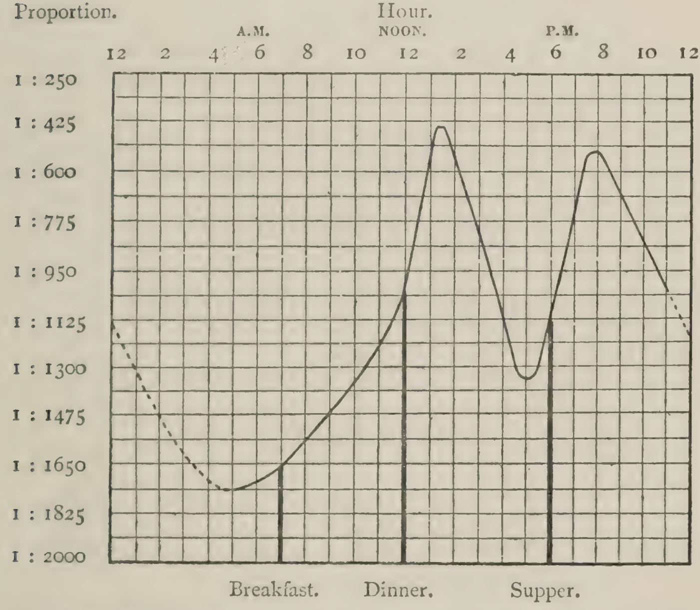
The increase of leucocytes commences about an hour after food, reaches its maximum at the third or fourth hour, and then gradually disappears. It is especially noticeable after a meal consisting largely of proteid substances. The occurrence of a multiplication of white corpuscles in the blood in

man, and in *carnivora* and *herbivora*, commencing a short time after the ingestion of food, must be regarded as a result of assimilation of nutritive products which the amœboid cells can make use of to a certain extent while they are circulating in the blood-stream as it passes through the abdominal vessels, the lymphatic duct, and, the usual site of white cell formation, bone-marrow and lymphatic glands. The principal causes, according to

CHART XII.—Showing Digestive Leucocytosis in Man.

Proportion of White Corpuscles to Red throughout the day (data by Hirt).

Normal Proportion—1 : 500.

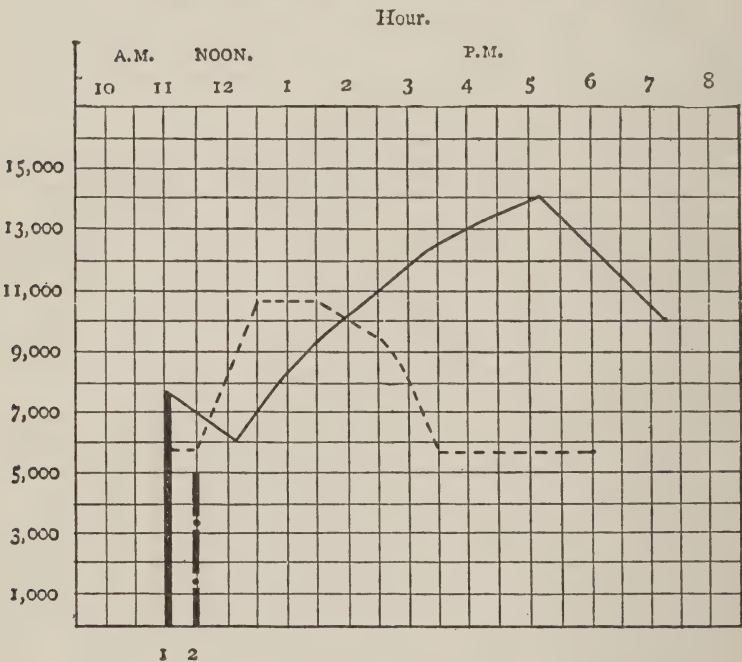


Ascoli (*Il Policlinico*, Nov. 15, 1896), are the increased stimulation of the abdominal circulation during active assimilation, and the consequent congestion of the blood-vessels distributed to the intestinal organs; and secondly, and a little later, the stimulation of the blood-forming apparatus by the absorbed material inducing an increase of chemio-taxis. As the white corpuscles are practically unicellular organisms contained in the circulating fluids of multicellular animals, there can be no inherent obstacle to the acceptance of the hypothesis that they can assimilate directly, even while *in transitu*, properly prepared nutriment should it be afforded them, nor can it be denied that, given such increment, the white

cells possess the power of karyokinetic or intrinsic multiplication. The point which as yet remains undecided is the site of this multiplication, but it appears probable that, although the chief sites are bone-marrow, lymphatic glands, and adenoid tissue, whether diffuse or aggregated into Peyer's Patches and similar bodies, the hyper-leucocytosis which accompanies active digestion originates largely in the blood-stream itself.

CHART XIII.—Showing Digestive Leucocytosis in Man.

Actual Increase in Numbers. (Data from Limbeck.)



Both subjects had fasted for 18 hours; at 11.15 (1) and 11.30 (2) were given food.

Actual number of Leucocytes per cubic millimetre.

——— First Subject.

- - - - - Second Subject.

Meal of First at 11.15.

Meal of Second at 11.30.

CHAPTER XIII.

THE SENSES.

SMELL :—Mechanism—Acuity—Taste largely smell.
TASTE :—Different tastes—Minimum amounts of substances required—Connection of sense of taste with habits and appetite.
HUNGER :—Nervous origin—Cause.
THIRST :—Local sensations—Nervous origin—Connection with hunger.

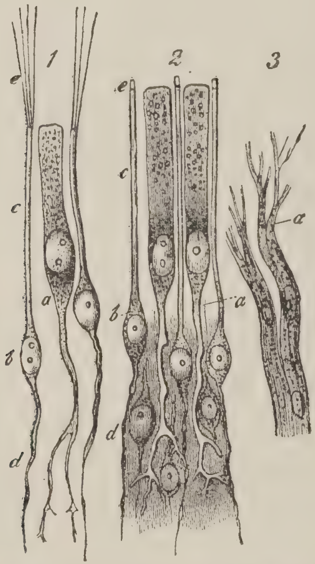
Smell.—The sense of smell is comparatively slightly developed in civilised man. The savage, and even a civilised man who has lived from his earliest youth in the open air, have much more sensitive olfactory organs. But even their power of smell is insignificant when compared with that of the dog or the deer.

Kant labelled smell "taste at a distance," and he was justified in doing so by the close connection which exists between the two. The stimulation of the terminations of the nerve fibrils supplied to the mucous membrane of the nose from the olfactory lobes of the cerebrum by volatile and soluble substances, constitutes the sensation known to us as smell. The exact intra-cerebral course of the fibres is as yet doubtful, but they may come from a centre in the tip of the uncinate gyrus on the inner surfaces of the cerebral hemispheres. The olfactory fibres are distributed over an area of the nasal mucous membrane known as the *regio olfactoria;* the remaining part is termed the *regio respiratoria.* The entire nasal mucous membrane is called either the pituitary or the Schneiderian membrane. The mucous membrane which covers the *regio olfactoria*, generally comprising the upper part of the septum and of the middle turbinated bone, is thicker than elsewhere. It is lined with a layer of single cylindrical epithelium cells containing a yellow pigment, and between which peculiar spindle-shaped cells are placed, terminating in slender processes. The process which reaches the surface of

the mucous membrane ends in some animals in a projecting filament, very similar to that in the taste-buds (see Fig. 47 and Figs. 16 and 17). The inner extremity forms a thin beaded filament which is supposed to communicate indirectly with fibres from the olfactory nerve. Some of the cylindrical cells appear

FIG. 47.

THE TERMINAL CELLS AND NERVE-FIBRES OF THE OLFACTORY REGION.



(Quain, after Schultze. Highly magnified.)

1, From the frog; 2, from man; 3, from the dog.
a, Epithelium cell with blunt outward end, and long inward process branching at its extremity; in 3, *a* shows the division of nerve-fibres into fine fibrils; *b*, olfactory cells, showing peripheral rods, *c*; outer extremities, *e* (in 1 prolonged into fine hairs), and central filaments, *d*.

also to be connected with nerve terminations, and the special name of *olfactory cells*, which has been applied to the spindle cells, would seem to be equally applicable to both forms.

In all mammals a subsidiary organ of smell is to be found, *Jacobson's Organ;* though rudimentary in man, it is highly developed in some animals. Both in the rabbit and guinea-pig

it is of relatively large size, and is supplied with fibres from the olfactory nerve.

The olfactory nerve is absent in *Cetacea*, and other aquatic mammals, and the nose is simply of use in respiration.

A sensation of smell is caused by contact with odorous particles, which must be volatile to enter the nasal cavity, and soluble to pass into the fluid which always covers the nasal mucous membrane. As the olfactory area is situated over the upper part only of the nose, the best means of detecting the presence of odorous particles is by a sudden sniff, or by a series of short inspirations. The sensation is only developed at the first contact, the perception of the odorous particles lasting only for a short time, unless the air containing them be drawn in afresh in separate amounts. It is a well-known circumstance that the continuance of a pleasant or even of a very foul odour soon causes a loss of its perception in one subjected to it, though departure from the impregnated atmosphere for a brief period suffices to again permit of its cognisance on return. Odorous substances dissolved or suspended in non-irritating fluids can be detected if sniffed up the nostrils, or if the nose be filled with them. This fact was long denied, but must at least hold good in fish, who can find their food, or a bait, in the dark by the sense of smell.

Much misconception exists with regard to the different classes of substances which possess the power of stimulating the olfactory nerves. The only substances which can cause strictly olfactory sensations are the non-pungent scents or perfumes. All others affect the tactile nerves as well as the olfactory, or act on the tactile fibres alone. Thus the odour of menthol can be detected by the olfactory nerves at the same time as the tactile fibres record first irritation, then numbing of their terminations. Acetic acid acts in the same way; while carbonic acid gas produces what seems to be the result of olfactory stimulation, but is really an excitation of the tactile fibres only. Electrical currents passed through the olfactory membrane give rise to a smell like that of phosphorus. In *Invertebrata* no organ of smell has been accurately recognised, but many of *Insecta* possess the sense. Perhaps it is located in their antennæ. The nostrils in fish lead into cul-de-sacs, not communicating with the alimentary canal. The lower of these sacs are thrown into folds, to the cells over which nerve-fibres pass from the olfactory lobe.

In *Amphibia* the nasal cavity is of simple design, but Jacobson's organ is well developed, while in *Reptilia* two canals open externally and internally into the mouth by passing through the palatine arch. In *Aves* the high development of the sense of sight compensates for comparatively poor olfactory power. The nares communicate posteriorly by slit-like apertures with the auditory cavities. In birds of prey and fish-eating *Palmipedes* the olfactory lobes are larger than in other species. Of *Mammalia* little need be added to the foregoing description. In many mammals, the hog, elephant, and tapir for instance, the nose is adapted for the prehension of food as well as for olfaction.

The sense of smell aids animals in their search for food and in their endeavours to avoid enemies. The dog or the antelope may be said to live in "a world of smells." The domesticated dog has been enabled to increase his sense of sight, but this still remains very inferior to his olfactory powers. Smell is concerned as much as taste in the perception of flavours. The volatile odorous particles of the food ascend by the posterior nares to the olfactory region and are there perceived, but, as is perhaps natural, the resulting stimulation is ascribed to the gustatory organs. The professional "taster" of teas or wines is aware of this, and takes care that the volatile bodies producing the flavour or "bouquet" have free access to the nasal chambers. The child who cheerfully swallows a dose of nauseous medicine when his nostrils are closed, and the man who is unable to detect the flavour of his food owing to nasal catarrh, afford practical illustrations of this fact.

Taste.—The structure of the lingual apparatus for the reception and transmission to the brain of the gustatory sensations produced by various substances has already been described. The lingual nerve contains the nerve-fibres of taste for the tip of the tongue, the glosso-pharyngeal those for the posterior part. Section of either nerve abolishes the sense of taste from the portion supplied by it.

Four varieties of taste can be distinguished, bitter, sweet, acid, or saline. What is commonly known as "flavour" is composed of one or more of these "tastes" coupled with stimulation of the sense of smell. For a substance to cause gustatory stimulation it must be soluble.

The tip of the tongue appreciates sweet and acid tastes better than the base, bitter tastes not so acutely. Experiment

has shown that some tastes are produced by more dilute solutions of their causal agents than others. An acid taste is appreciated in solutions of the greatest dilution; bitter, saline, and sweet tastes require the presence of progressively larger amounts of the active ingredients before they can be distinguished.

TABLE LII.—*Showing the Maximum Dilution at which the various Tastes are Appreciable. (Data from Valentin.)*

Substance.	Character of Taste.	Strength.	Amount of Fluid necessary.	Total Substance in Solution Tasted.	Intensity of Taste.
			c. cm.	Grammes.	
Sugar - -	Sweet	$1/_{83}$	20	0.24	Faint
Salt - - -	Saline	$1/_{213}$	1.5	0.007	Pronounced
,, - - -	,,	$1/_{426}$	12.0	0.027	Faint
Aloes - -	Bitter	$1/_{323}$	0.25	0.0008	Very pronounced
,, - - -	,,	$1/_{12500}$	10	0.0008	Perceptible
,, - -	,,	$1/_{900\,000}$	—	—	Faint after-taste
Quinine Sulphate	,,	$1/_{33\,000}$	—	—	Pronounced
,, ,,	,,	$1/_{1\,000\,000}$	—	—	Trace
Strychnine - -	,,	$1/_{40\,000}$	—	—	Strong
,, - -	,,	$1/_{400\,000}$	—	—	Pronounced
,, - -	,,	$1/_{640\,000}$	—	—	Perceptible
Sulphuric Acid -	Acid	$1/_{100\,000}$	—	—	Pronounced
,, ,,	,,	$1/_{1\,000\,000}$	—	—	Absent

TABLE LIII.—*Showing the Relative Accuracy in the Power of Distinguishing Bitter and Saline Substances in Various Degrees of Dilution.* 30 *c. cm. taken each time. (Data from Camerer.)*

Amount of Substance in 30 c. cm.		Degree of Dilution.	Percentage of Correct Perceptions.
	in grms.		
Quinine Sulphate	...0.089	$1/_{34000}$	89
,,	...0.074	$1/_{40\,000}$	88
,,	...0.059	$1/_{51\,000}$	77
,,	...0.044	$1/_{68\,000}$	62
,,	...0.029	$1/_{103\,400}$	32
Chloride of Sodium	...28.600	$1/_{1049}$	100
,,	...19.100	$1/_{1562}$	86
,,	..14.300	$1/_{2098}$	80
,,	... 9.500	$1/_{3125}$	49
,,	... 4.800	$1/_{6250}$	9

Quinine is about twenty times more powerful a gustatory stimulant than common salt. The time which elapses, the "reaction period," between the contact of substances with the taste papillæ and their appreciation varies with their characters.

TABLE LIV.—*The Periods of Time, in Fractions of a Second, which elapse before the Brain perceives the Taste of various Substances placed upon the Tongue.*

Substance.	Taste.	Reaction-period when placed on tip of Tongue. Seconds.
Chloride of Sodium	Saline	0.1598
Sugar	Sweet	0.1639
Acids	Acid	0.1676
Quinine	Bitter	0.2196
Direct Touch	—	0.1507

When the cathodal end of a galvanic circuit is placed on the tongue, the passage of the current produces an acid taste; the anode similarly applied gives rise to a metallic bitter taste.

The sense of taste in *Invertebrata*, when present, must be located about the mouth, in the proboscis, suckers, or other processes, for they do not possess any organ analogous to a tongue. Fishes have either little or no sense of taste. Their tongues are rudimentary, horny or even covered with small teeth. Their isolated olfactory cavities may serve as taste organs as well as for smell. Judging by what such a fish as the cod will swallow, its taste sense must surely be of a most catholic character.[1] As birds swallow their food whole, an acute sense of taste is unnecessary. In graminivorous birds the tongue is hard and horny and precludes the probability of it being of use for tasting; carnivorous birds, with fleshy tongues, may be supposed to possess some power of taste.

The senses of taste and smell in *Mammalia* exhibit numerous variations, the reason for which remains unknown. The *Herbivora* assuredly take pleasure in the taste of grass, hay, or corn; a horse prefers oats to hay, and hay to straw; but normally to all *Herbivora* the taste of flesh is abhorrent, save during the period following on the birth of their young. Curiously, it is during the same period that women so often display likings for articles which at other times would prove nauseating. The rabbit and the sow will devour their off-

[1] The author has personal knowledge of boots and puppies being found in the stomach of large cod!

spring; women will crave for or eat ashes, slate pencils, and filth of every description. The general phenomena of the likes and dislikes of an animal towards articles of food are closely correlated to the nutritional needs of its body and to the digestive powers of its alimentary canal. But even in members of the same species there is a marked difference in the pleasure or dislike originating in the smell or taste of different substances. In man, in whom civilisation has often rendered the balance of the nervous system unsteady, a certain smell or taste has been known to cause fainting and nervous upset on every occasion on which it has been encountered. The intimate relationship of these two senses to the alimentary system and to cerebral processes; their adaptation to the requirements of bodily metabolism; their development as means of defence against danger; and their peculiar variations in different species or individuals, mark them out as the outcome of mechanisms developed by long-continued habit and need, which are closely bound up with the inner life of beings, and differ with the individual requirements of each. The eye and the ear differ little in structure and arrangement, or in their powers, save in acuity, among the higher animals; taste and smell vary as to the mental processes originated by them in almost all species.

Hunger.—As sleep is the cerebral indication of a general sensation of weariness, so hunger is a signal, localised near the region of the stomach, but given by the brain, indicative of a general impoverishment of the circulating fluids in the body. Over-exertion may inhibit sleep, notwithstanding intense weariness, through an excess of metabolic products in the blood; various states of mental excitement act similarly. The sensation of hunger arises whether the stomach be full or empty. In the rabbit and guinea-pig the stomach never empties, the newly-swallowed food serving to drive the contents downward, but the starved rabbit exhibits signs of hunger. The *Carnivora* do not suffer from the sensation of hunger until hours have elapsed after the stomach has become empty. Many general conditions influence the sensation. Many drugs act on the nerve centre involved, and diseases often act in the same way, preventing the onset of the sensation, while other maladies cause increase of the hunger sense, or even *bulimia.* All these conditions act by influencing the blood-supply to the central nervous system, causing con-

sciousness of a state of bodily nutrition different from, or opposite to, the actual facts. Many have sought to prove that hunger arises locally; that it is due, principally at any rate, to immediate influences acting on the stomach walls Nearly all the evidence obtainable is against such a view. Solid indigestible bodies, or water, introduced into the stomach often do arrest the feeling of hunger, but only temporarily; while injection of nutritious fluids into the blood, or as enemata into the rectum, abolish it.

Pigeons and frogs deprived of their cerebral hemispheres for long exhibit no desire for food; but Ewald observed a pigeon treated thus begin to take food voluntarily after a period of eleven months, and saw frogs, devoid of their cerebra, catching and devouring flies in a normal manner. Section of the vagi and sympathetic nerves going to the stomach does not abolish hunger, so that no nervous connections between the brain and that organ are necessary for causation of the sensation.

Hunger, then, may be regarded as a manifestation by the central nervous system below the cerebrum, probably by a centre in the medulla, of an impoverished state of the blood; exhibited more or less locally in the gastric region, and arrested, temporarily by mechanical filling of the stomach, or by pressure over it, gradually by the ingestion of food, and rapidly by the injection of nutriment into the blood-stream. The controlling hunger-centre in the medulla regulates the excitation of the centres by which the symptoms are initiated.

Thirst.—The mechanism involved in the causation of the feeling of thirst very closely approximates in its arrangement to the apparatus which brings about hunger. The resulting sensation is more localised, only being perceived over the fauces and pharynx. Application of water to this region temporarily quenches it, as does the passage of saliva over it. As the period of abstention lengthens, the secretion of saliva diminishes, while it becomes less fluid and less capable of satisfactorily acting on the mucous membrane. It is well known that a pipe of tobacco, by increasing the flow of saliva, often proves of use when thirst is present and cannot be quenched for some time; but its influence lasts only during the act of smoking. Fluids, when drunk alone, rapidly pass through the stomach, and are absorbed by the bowel. Solids do not enter the blood-

stream so quickly. Thirst, therefore, is quenched sooner than hunger is satisfied. Fluid taken with solids does not satisfy thirst so soon as if taken alone; but as it passes out of the stomach in small quantities sooner than the mass of the solid food, the sensation of thirst, though not so quickly abolished as when fluid is taken by itself, tends to disappear before that of hunger. Continued deprivation of water and solid food together does not rouse so acute a feeling of thirst as deprivation of fluid when dry solid food-stuffs are taken. As hunger advances, the water excreted only corresponds to that contained in the tissues actually broken down; the percentage of water in the remaining tissues does not alter. A dog during the later stages of starvation will not drink the water offered to it.

Thirst can be alleviated by the subcutaneous injection of water, or by rectal injections, and is only a local expression of the irritation of a centre in the brain owing to a diminution in the proportion of water in the blood. All conditions tending to withdraw water from the blood favour the appearance of thirst; warmth, exercise, fevers, diabetes, loss of blood, or ingestion of much salt act thus.

CHAPTER XIV.

Metabolism in Animals.

Metabolism:—Definition—Food Constituents—Metabolism of Proteids—Living and Dead Protoplasm—Urea—Seat of Urea Formation—In the Liver—Uric Acid—Hippuric Acid—Muscular Work and Metabolism of Proteids.
Metabolism of Carbo-hydrates:—Glycogen—Diabetes Mellitus—Oxidation of Sugar in Active Muscle—Formation from Proteids, from Carbo-hydrates.
Metabolism of Fat.
Inorganic Salts:—Iron—Metabolism during Starvation.

The term metabolism includes all the chemical processes taking place in the body by which the available elements of the food are prepared for nutrition, changed for incorporation into the tissues and fluids, used up for the purposes of movement or vitality, and finally altered into forms capable of excretion.

To understand fully the processes of metabolism in the animal body we must first consider the part which the different elements of the food play in them. As the food ingested is intended to provide all the necessary constituents of the different tissues of the body, and as different animals and even different races of mankind use different food-stuffs, the subject perforce is a very complicated and difficult one. It has already been shown that the necessary constituents of the food must be capable of supplying a sufficient quantity of the elements, nitrogen and carbon, and of mineral salts and water, to satisfy the wants of the various formed tissues and fluids of the body, while the necessary food substances have already been divided into five classes: proteids, fats, carbohydrates, salts, and water. If we consider the part which each class of food-stuff plays we find that—

1. The proteids are a source of energy, and contribute to form and keep up the primary or active protoplasm of cells, and their accessory or inactive constituents.

2. The fats are also a source of energy, and may supply a portion of the inactive material composing the cells.

3. The carbo-hydrates have similar functions to those of the fats.

4. The mineral salts are not producers of energy in the body, but are indispensable both for the active or protoplasmic part and for the inactive framework of the cell.

5. Water acts as a general solvent and necessary agent for the different metabolic processes.

Proteids, water and mineral salts are absolutely necessary for the preservation of the life of all animals. Proteid substances can be so altered in the body as to supply both fats and carbo-hydrates when required; the converse does not apply. The animal body is unable to produce proteids from either fats or carbo-hydrates. On the other hand, as these two classes of food-stuff act as sources of energy, if they be given along with proteids they will serve to diminish the amount of albuminous food necessary. That is to say, they act as proteid-sparing bodies. An animal fed upon proteid alone requires more proteid than one fed upon a diet of proteid mixed with either fats or carbo-hydrates. With such a mixed diet the animal draws some of the energy required for its various bodily functions from the fats or carbo-hydrates instead of from the proteids assimilated from its food. Neither of these two classes of food elements contain nitrogen; they can serve, however, as sources of energy. Nitrogenous substances are not essential in the performance of physical bodily functions. The carbon in fat and carbo-hydrates, uniting with the oxygen conveyed in the blood, can produce the requisite amount of energy required for animal life; but, as nitrogen is absolutely essential for the formation of protoplasm, and as protoplasm is the primary agent in all living processes, the fats and carbo-hydrates alone are not sufficient to support life.

When an animal is said to be in a state of nitrogenous equilibrium the output of nitrogen in the various excretions is exactly the same as that taken in with the food. In this condition of nitrogenous equilibrium, however, it is necessary to give two and a half times the amount of proteid corresponding to the nitrogen which would be eliminated in an animal after it

had been starved for a short time. This fact shows that all the proteid in the food cannot be used to replace the nitrogenous tissues disintegrated in the body. To explain this difference in the amount of nitrogen arising from tissue waste and eliminated, and the nitrogen contained in the food, it has been suggested that part of the proteid taken goes to form the living cells of the body or to replace their waste, and part to form the unorganised proteid circulating in the blood and other fluids of the body. The part which is supposed to circulate in the juices and to bathe the protoplasmic elements of the cells is said to be rapidly broken up into derivatives of a non-proteid character without having ever formed part of the protoplasm of the cells. The disintegration of this circulating proteid is very much more rapid than of that which goes to form the tissue cells. Voit found that a large dog during starvation only eliminated each day as much nitrogen as corresponded to 1 per cent. of the living cell material of its body. In men of normal adult weight, kept without food, the daily destruction of proteid is generally about 33 grammes, corresponding to a loss of 5.25 grammes of nitrogen. If we consider that the destruction of the tissue proteid during starvation is more than double the normal, a fact which has been shown to be true in the dog, the amount of tissue proteid used up each day in the healthy adult man will be 16 grammes. The circulating proteid, under normal conditions, must therefore yield 16 grammes to the tissues each day for the purpose of rebuilding this loss. In addition to this a certain amount will be required for the growth of new cellular elements. Thus we may presume that in man when the amount of proteid assimilated exceeds 16 or 17 grammes per diem, the excess may be transformed into fats, carbo-hydrates, and nitrogenous derivatives, of which the first two are made use of as sources of energy.

Moleschott has estimated the total amount of water in the tissues of the human body as 68 per cent., the proteid and other nitrogenous substances as 20 per cent., while Voit gives the amount of fat as 18 per cent. The different organs contain very varying proportions of water: thus the enamel of the teeth contains only 2 per cent., the muscles 75.7 per cent., and the blood 79 per cent. Roast beef contains as much as 72 per cent. of water, milk 87.4 per cent., and white of egg 85.7 per cent.

The metabolism of a single living cell, whether it forms an entire individual, as *Amœba*, a congeries of practically inde-

pendent cells as in the *Polyps*, or one of the myriads which go to make up the higher animal beings, is exactly alike. In the unicellular organism, such as *Amœba*, the food taken in is assimilated by the single cell and applied by it in the production of energy for the growth of its body and the repair of any of its substance used up during the outcome of vital activity. The same is true of all the cells which, when segregated together, go to make up a multicellular organism. As we ascend the scale of the animal kingdom we meet with complex organisms formed of numberless cells, some of which are capable of one function, some of another, and others which are practically passive. The single cell of an *Amœba* requires the same proportion of food elements as the entire body of a higher animal type, the same, indeed, as is necessary for the maintenance of the life of man. In such a single living cell the elements of nutrition are used to nourish and vivify the cell itself. In more complex animal organisms the food elements absorbed are used by the protoplasm of the various kinds of cells in very different ways. There is no rule by which we can say definitely that such a molecule of proteid matter will go to aid in the nourishment of, say, a brain-cell, or that such another particular molecule will find its resting-place in the protoplasm of a bone-forming, a gastric, or a splenic cellular unit. In whatever form the proteid or the carbohydrate molecule is present in the food, it may serve, thanks to the changes brought about by digestion and to the vital power of protoplasm, as an addition to the body-proteids in any kind of cell, or be used up in the production of heat or energy.

The subject of animal metabolism is so complex that it will facilitate matters to consider the changes which take place in each of the classes of proximate principles *seriatim*, and then to sum up the information gained in a review of the general process.

Metabolism of Proteids.—The different proteids contained in the various tissues and fluids of the body are derived from the proteid products of digestion which have been absorbed from the alimentary tract. The two chief proteid bodies in the blood-plasma are serum-albumin and serum-globulin. The exact site of their formation is supposed to be in the intestinal mucous membrane during the passage from the canal into the blood-stream. The proteids absorbed from the alimentary

canal are chiefly in the form of albumoses and peptone. Although they are absorbed in those forms by the mucous membrane, the blood which nourishes the walls of the tract does not contain much more peptone or albumose than the blood passing through other parts of the body. These substances then, it is clear, must be altered during their passage through the epithelium lining the alimentary tract, and be transformed into serum-albumin and serum-globulin. The importance of this change will be recognised when it is stated that the presence of peptone and albumose produces grave alterations in the blood, causing it to lose the power of coagulation, and inducing symptoms of active poisoning throughout the body generally. A description of the difference between living and dead proteids contained in Dr. Stewart's *Manual of Physiology*, 1895, is so apt that I need make no apology for quoting part of it:—"Now and again a living proteid molecule in the whirl of flying atoms which we call a muscle-fibre or a gland-cell, or a nerve-cell, falls to pieces. Now and again a molecule of proteid, hitherto dead, coming within the grasp of the molecular forces of the living substance, is caught up by it, takes on its peculiar motions, acquires its special powers, and is, as we phrase it, made live. But it is not any difference in the kind of proteid which determines whether a given molecule shall become a part of one tissue rather than of another. For it is from the serum-albumin and serum-globulin of the blood that all the proteid material required to repair the waste of the body must ultimately be derived; and a particle of serum-albumin may chance to take its place in a liver-cell and help to form bile, while an exactly similar particle may become a constituent of an endothelial scale of a capillary and assist in forming lymph, or of a muscular fibre of the heart and help to drive on the blood."

Indeed, members of the same species are fashioned in each other's likeness from very different foods, or again, different species present strongly contrasting attributes though subsisting on the same diet. In the first case, we can find a parallel by taking as an example men's habitations; all those built of stone have a certain resemblance to each other, and differ from those constructed from wood or other material. Using the same illustration, those buildings constructed with stone may differ in detail; one may be a dwelling-house, another a church, and yet another a lighthouse. Similarly, various

breeds of dogs may be reared on the same diet, while the same diet, given to another animal, suffices for its nutrition in a perfectly normal manner. We may safely affirm that no change in the character of the food is able to radically alter the structure of any of the more highly organised tissues of the body. The individual cells may be fed with different food-stuffs, may be overfed, or may even be starved, without any change in their essential features as long as they possess life. This leads to one of the most difficult questions in all physiology. The further the science advances the more remote does the possibility of our being able to determine what the difference between a living and a dead cell consists in. Pflüger has suggested an ingenious theory to account for the alterations in the characters of living and dead protoplasm. Living protoplasm is a complex substance of great instability; the molecules forming it possess great powers of movement and of dissociation. When dead the same substance is more stable and inert. Pflüger ascribed the instability of living protoplasm to the presence of the nitrogen in the form of cyanogen radicals, the atoms of which are able to move about in the molecule with great facility; while in dead proteid the nitrogen takes the form of amides. Similarly, Loew and Bokorny have suggested that the characteristics of living protoplasm depend on the presence of the unstable aldehyde group, $H-C=O$. Whatever the cause may be, the proteid of living protoplasm can split up into smaller molecules and can reconstruct other forms of matter, faculties which dead proteid bodies do not possess. The living proteid breaks down in the body more easily than dead proteid molecules outside it, but it falls to pieces in a fairly constant manner, giving rise to carbonic acid, water, and simple nitrogenous substances such as urea, uric acid, and ammonia, with the help of the oxygen present in the blood-stream.

It is an interesting question, which goes, however, beyond the province of this book, how far living protoplasm corresponds in chemical composition to uncoagulated native proteids removed from the tissues. It is impossible, of course, to analyse living protoplasm, as the chemical processes which it has to undergo during analysis necessarily involve its death. Protoplasm and native albumins, however, correspond very closely in their elementary constituents: they both present all the reactions

which indicate a native proteid, and both invariably contain a certain percentage of inorganic salt. The fact that so-called ash-free albumins and globulins have been artificially obtained outside the body in no way detracts from the accuracy of this statement, as the reactions of these ash-free bodies present many points of difference from those of the ordinary native albumins.

(1.) *The Formation of Urea.*—By far the largest proportion of the excreted nitrogen leaves the body of the mammal in the form of urea, although in cold-blooded animals, and in birds, uric acid, which is probably a preliminary stage in the formation of urea, takes its place.[1] In the *Herbivora* hippuric acid may be said to take the place of uric acid in its turn. Urea is contained in small quantities in the blood, from 2 to 4 parts per 10,000. Some of the urea excreted by the kidney may therefore be simply separated by that organ from the blood, and this has been shown to be the case in so far as the blood in the renal vein running from the kidney always contains a little less urea than the blood of the renal artery. If we could exactly measure the difference between the proportion of urea in the renal vein and renal artery, and, therefore, the loss occurring in the kidney during the course of twenty-four hours, we should be able to tell exactly the amount eliminated in that period of time, and to tell by the amount of urea found in the urine whether a process of separation is the only one at work. Voit found that a dog of 35 kilogrammes weight, and receiving a sufficient proteid diet to maintain its weight (500 grammes of lean meat per day), excreted 40 grammes of urea in the twenty-four hours. He then calculated the total quantity of blood which would be circulating in a dog of this weight, and, assuming that the average time required for the blood propelled by each beat of the heart to pass through the kidney was 10 seconds, he arrived at the conclusion that 300 kilogrammes of blood passed through the kidneys in twenty-four hours.

[1] Tschlenoff has found that the increase in the excretion of nitrogen in the urine does not proceed uniformly after a meal rich in proteids, but shows two maxima. Veraguth lately (*Journ. of Phys.*, xxi. 2 and 3, p. 112, 1897) has repeated Tschlenoff's experiments, and finds three maximal periods during which the nitrogen excreted in the urine increases in a more marked manner than during the intervening periods. The first occurs soon after food is taken; the second two to four, and the third six to seven hours later. If the food taken contains less proteid these maxima are still perceptible, but are not so prominent.

Therefore, if the blood contain .3 per 1000 of urea, the total weight of urea which would circulate through the kidney during that time would amount to 90 grammes. But only 40 grammes were excreted in the urine. The kidney epithelium actually came in contact in the twenty-four hours with more than double the quantity of urea that it actually separated from the blood.

The urea may be formed, to some extent, in the kidney itself, but ligature of both renal arteries in the dog does not prevent the accumulation of urea in the blood, and the amount of accumulation appears to be very similar to that which the animal would excrete under normal circumstances. Little urea, therefore, can be actually formed in the kidney substance.

The liver is the chief seat of urea formation from the *débris* of broken-down nitrogenous bodies brought to it by the blood. It acts, in fact, as a factory in which the nitrogenous remains of the proteid waste of the body are simplified through several stages into the final product of urea.[1]

The facts which point to the liver acting in this way are—

1. Leucin, if taken in large quantities, is excreted by the kidneys as urea, while in certain diseases of the liver, such as acute yellow atrophy and advanced fatty degeneration, where the liver tissue is much altered, the urea excreted in health may be almost entirely replaced by leucin and tyrosin.

2. If a solution of ammonium carbonate be mixed with defibrinated blood and passed through the vessels of a liver recently excised, urea is formed in quantity, although none appears to be produced from ammonium carbonate when similarly sent through an excised kidney or through muscle.

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[1] Recent observations by Nencki and Pawlow (*Arch. f. Experim. Pathol. u. Pharmakol.*, xxxviii., 3 u. 4, p. 215, 1897), however, serve to throw doubt upon the liver being the exclusive source of urea in the body. These observers experimented on healthy dogs abundantly fed with meat. They established in them a communication between the portal vein and the inferior vena cava (Eck's venous fistula), and then extirpated the liver as completely as possible. This proceeding should be followed by an increase of the ammonia excreted by the urine, and a diminution of the urea if the liver be the sole source of urea. In the first dog operated on, the ammonia in the blood and urine was increased in amount, and the urea decreased; but in the second dog the quantity of urea in the blood, and of ammonia in the blood and urine, was increased. In a third dog, in which the blood of the portal vein was diverted into the inferior vena cava, the liver was not removed, but the hepatic arteries ligatured; the proportion of urea in the blood remained unchanged. Nencki and Pawlow conclude that the liver cannot be regarded as the sole urea-forming organ or tissue of the body of mammals.

3. If blood taken from a dog, killed during the process of digestion, be passed through an excised liver, some urea is formed, while the blood of a fasting animal treated in the same way yields none. This experiment shows that the blood of an animal during active digestion must contain certain substances in considerable quantity and in excess of the amount which the liver is able to convert into urea during their progress through it until this has been repeated many times. For in birds uric acid, which, as we have seen, takes the place of urea and forms the chief ultimate product of the metabolism or breaking-down of proteids, is certainly produced almost exclusively in the liver.

Minkowski, taking advantage of the fact that there is a direct communication in birds between the portal and the renal-portal veins, extirpated the entire liver in living geese. After this operation the blood from the alimentary canal passes by a devious route through the kidney to the inferior vena cava, and the animals can survive from 6 to 20 hours. The uric acid excreted after this operation contained only 3 to 6 per cent. of the total nitrogen excreted in the urine, the nitrogen given off as ammonia from 50 to 60 per cent. of the nitrogen. In a normal goose, the uric acid eliminated contains 50 to 60 per cent. of the total nitrogen in the urine, and 9 to 16 per cent. is in the form of ammonia. The small amount of urea, which is normally present in the excretion of the bird, is not affected by the excision of the liver, but urea injected into the blood after such an operation is excreted unchanged, although it appears as uric acid in a normal animal.

The foregoing evidence is sufficiently convincing to allow of our definitely stating that the liver is the chief seat of the final disintegration of proteid molecules. It is not, however, the only organ or tissue in which proteid changes can occur. In all the parts of the body which contain proteid—and every part contains it in some form or other—proteid molecules are ever breaking down; the local products of this destruction of proteids are less oxidised and more complex than urea, and are probably intermediate stages between the complete proteid and urea, stages which are progressive and result in a series of nitrogenous bodies which become more and more simple and contain more and more oxygen, until they pass, through the action of the hepatic cells, into the final form of urea. Some of these substances are given in Table LV.

It will be seen from the table that the proportion of nitrogen to oxygen is about 1:1.4 in native proteids; and that this proportion rises rapidly in the series from guanin to uric acid from 1:0.228 to 1:0.857. Kreatin is contained in the body in much greater amount than any of the others, muscle containing as much as 0.4 per cent. of it. Bunge has suggested that it may be one of the stages on the way to urea, as it forms one of the series represented by the substances which constitute the medi-

TABLE LV.—*Showing the Molecular Constitution of Proteids and several of their Derivatives.*

	Atoms of Carbon.	Atoms of Hydrogen.	Atoms of Nitrogen.	Atoms of Sulphur.	Atoms of Oxygen.	Molecular Weight.	Percentage by Weight of Nitrogen.	Percentage by Weight of Oxygen.	Proportion of Nitrogen to Oxygen by Weight. N. O.	Heat Equivalent. Large Calories.
1 Hæmoglobin ...	712	1130	214	2	245	16,710	17.94	23.42	1–1.33	
2 Albumin[1]	680	1098	210	2	241	16,118	18.2	23.9	1–1.31	4,998
3 Tyrosin	9	11	1	—	3	181	7.73	26.5	1–3.4	
4 Leucin	6	13	1	—	2	131	10.6	24.4	1–2.28	6,141
5 Asparagin... ...	4	8	2	—	3	132	21.2	36.3	1–1.71	
6 Lysin	6	14	2	—	2	146	19.1	21.9	1–1.14	
7 Lysatinin	6	11	3	—	1	141	29.0	11.34	1–0.38	
8 Glutamic acid ...	5	9	1	—	4	147	9.5	43.5	1–4.57	
9 Guanin	5	5	5	—	1	151	46.3	10.59	1–0.228	
10 Hypoxanthin ...	5	4	4	—	1	136	41.1	11.76	1–0.285	
11 Xanthin	5	4	4	—	2	152	36.8	21.05	1–0.57	
12 Uric acid	5	4	4	—	3	168	33.3	28.5	1–0.857	2,615
13 Kreatin	4	9	3	—	2	131	32.06	24.4	1–0.759	4,118
14 Kreatinin	4	7	3	—	1	115	36.5	13.9	1–0.38	
15 Urea	1	4	2	—	1	60	46.6	26.6	1–0.57	2,200

[1] From the blood of the horse (Zinoffsky).

ate members of the table. Kreatin, however, does not appear to be changed in any quantity into urea in the body. The only member of this class about which there is conclusive evidence is uric acid, and it appears certain that it is one of the stages lying between the complex proteid molecule and simple urea. Amido-acids have also been said to form intermediate substances in proteid destruction, but Bunge has shown that there is not enough carbon in the proteid molecule to convert all the nitrogen present into amido-acids. When these substances are given by the mouth, however, the output of urea is increased, although the increase is less than corresponds to the amount of their nitrogen. Some of it must therefore be used up in other ways in the body, and Lea has suggested that amido-acids act as agents in the liver, taking part in the synthetic or constructive processes in that body, and so are not on the downward series of substances derived from proteid metabolism, but rather, as he terms it, on the upward grade.

An observation by Lieblein (*Arch. f. Exp. Path. u. Pharm.*, 33-4-5, s. 318), who destroyed the liver tissue in dogs by injecting acids into the common bile-duct, shows that under such conditions an increase occurs in the amount of uric acid excreted by the kidneys. The proportion between the nitrogen excreted as ammonia and the total nitrogen in the urine varied slightly, if at all, in direct contrast to the experiments noted above on geese. Gaglio (*Du Bois' Archiv.*, 1886, s. 400) has found that blood in the dog during the digestion of flesh contains 0.3 to 0.5 per thousand of lactic acid. During fasting this figure falls—for instance, it falls, forty-eight hours from the last meal, to 0.17 per thousand—but it never wholly disappears. He also observed an increase in the quantity of lactic acid in blood which had been passed through a recently excised kidney or through excised lungs. It is interesting to note that blood-serum is unable to remove lactic acid from the tissues, although, whenever the corpuscles are not removed from the blood, the amount of lactic acid invariably increases. In the experiments of Minkowski (*loc. cit.*) on geese, the ammonia excreted in the urine was found to be in the form of lactate, not as the usual carbonate, while the lactic acid and the ammonia were always present in amounts equivalent to their powers of combination. It is probable from these observations that ammonium lactate plays a part in the formation of uric acid in birds. It is also noteworthy that in

animals whose liver has been removed the quantity of lactic acid excreted is independent of the amount of carbo-hydrates in the food, but varies directly with the proteids taken. Araki (*Zeit. f. phys. Chem.*, Bd. 15, s. 335) has thrown still more light on this subject. He found that dogs, rabbits, and hens kept in an atmosphere poor in oxygen soon excreted ammonium lactate in the urine. We may safely say, therefore, that one of the forerunners of urea consists in lactate of ammonium, which can be transformed by oxidation into ammonium carbonate and then into urea.

(2.) *Uric Acid.*—Little need be added to our previous description of the formation of urea in dealing with its close ally, uric acid. In cold-blooded animals and in birds most of the nitrogen of the broken-down proteids in the body is excreted in this form. It seems best to look upon the formation of uric acid in man as a result of a certain type of proteid metabolism, resembling processes in animals in whom different physiological methods take place. The fact that in man a distinct uric acid diathesis (which is often hereditary) is met with, may perhaps point to some physiological reversion towards those lower forms in which this body is so abundantly formed under normal circumstances.

(3.) *Hippuric Acid.*—In the *Herbivora* this body replaces uric acid as one of the results of proteid metabolism. In man the ingestion of benzoic acid is followed by excretion of hippuric acid by the kidneys. Hay contains a benzoic acid compound, and it is not difficult to find in it one of the causes leading to the appearance of hippuric acid in the urinary excretion of the *Herbivora*.

(4.) *Kreatinin.*—We have little knowledge of the origin of this substance in the body. Kreatin can be very easily transformed into kreatinin by artificial means, but there is no evidence to show that such a chemical change really takes place in life in the body.

(5.) *Carbonic Acid.*—It cannot be definitely said whether carbonic acid, split off from the proteid molecule, is at once produced when the nitrogenous part of the molecule breaks down, or whether the carbon not utilised in the formation of the proteid derivatives forms other intermediate products, which may finally be excreted as carbonic acid. Of course, as we shall see shortly, some of the carbon may be retained in the body as glycogen or fat, and this, perhaps, may point

to a series of changes before the carbonic acid is finally excreted in its simple form. (Table LVI.)

The effect of muscular work on proteid metabolism, as shown by the observations of Krummacher (*Zeit. f. Biol.*, xxxiii. s. 108, 1896), is indicated by a slight increase in the destruction of body proteid, an increase not in proportion to the amount of work done, and least when the food is rich in non-nitrogenous material. Consideration of the calculated energy corresponding to the amount of proteid used up in the body shows that it cannot be produced to any great extent by proteid combustion during muscular work, and not at all from proteids under ordinary conditions.

TABLE LVII.—KRUMMACHER'S OBSERVATIONS.

Giving the results obtained in three series of observations upon the day on which work was done by subjects kept on uniform diet for eight days, with muscular work on the fifth.

	Diet in Grammes. Albumin.	Fat.	Carbo-hydrates.	Work in Kilogrammetres.	Percentage increase of Albumin destroyed on fifth day.
1.	95	88	303	153,070	23
2.	137	168	709	324,540	22
3.	89	175	903	401,965	7

	Percentage of Albumin in Diet.	Total Diet in grammes.	Calories.	Percentage of increase in Proteid Destruction.
1.	19	496	2,389,726	23
2.	13	1,014	4,854,618	22
3.	7·5	1,167	5,444,906	7

A recent paper by Noël Paton and others (*Journal of Physiology*, xxii., 1897) shows that increased amounts of proteid are made use of by the body under conditions of excessive muscular work. This proteid is chiefly derived from the muscles, because no increased excretion of uric acid or phosphorus takes place, muscle having little nucleo-proteid in it from which these substances can be derived. If the individual be in poor training, other tissues as well as the muscles are called upon for some of their proteid.

We may sum up our present knowledge of the metabolism of proteid bodies as follows :—

1. Nitrogen does not pass into the form of urea in the tissues themselves, but appears in the urine for the most part in this form as the result of changes effected principally in the liver.

2. Some of the nitrogenous elements of the food may be excreted as urea without having formed a part of the proteid constituents of the body. That is, nitrogen may be absorbed

TABLE LV *a Nitrogen Balance when at Rest and*

1. AT REST.

Fo	ference of ed Elements.	Increase in Body.
Total Weight		145.4 grammes.
Water - -	+19.24 H +153.76 O	
Carbon - -		
Hydrogen - -	—41.98 +19.3	Fat, 51 grammes. Water, 85.9 grammes. C 39.8 ,, — ,, H 5.85 ,, H 9.54 ,, O 5.35 ,, O 76.35 ,,
Oxygen - -	—236.6 +153.9	Leaving 7.31 H, 1.0 O.
Nitrogen - -		
Ash - - -		

2. AT WORK.

		Decrease in Body Weight.
Total Weight -		49.0 grammes.
Water - -	+48.17 H +385.4 O	Loss of
Carbon - -		Proteid, 266 grams. Fat, 34.6 grammes. C 0.138 grammes. C 26.99 ,,
Hydrogen - -	—40.99 +48.17	H 0.0186 ,, H 3.98 ,, N 0.04 ,, O 3.63 ,,
Oxygen - -	—371.32 +385.4	O 0.06 ,,
Nitrogen - -		Leaving 3.1814 grammes Hydrogen, and 10.39 ,, Oxygen.
Ash - - -		

3. DIFFEREN(

	OXYGEN (not in Water).		NITROGEN.		ASH.	
	ıken in	Excret'd	Taken in	Excret'd	Taken in	Excreted
Rest - -	920.6	684	19.47	19.47	23.9	24.0
Work -	217.75	846.43	19.49	19.53	24.88	25.3
Difference	297.15	+162.43	+0.02	+0.06	+0.98	+1.3

	ʒygen in Water.	Oxygen not in Water.	Nitrogen.	Ash.
Difference betwee	-153.76	+236.6	0	—0.1
Do. do.	-385.4	+371.32	—0.04	—0.42
Do. at Res	-231.64	—134.72	+0.04	+0.32

Table LVI.—*Showing the Metabolic Changes of the Food Elements sufficing in Man to maintain a Nitrogen Balance when at Rest and at Work. (After Voit.)*

1. AT REST.

Food Stuff taken in.		Excreted in: Urine.	Fæces.	Respiration and Skin.	Elements Excreted.	Difference of Excreted Elements.	Increase in Body.
Total Weight	3342.7	1343.1	114.5	1739.7	3197.3	—145.4	145.4 grammes.
Water	2016.3 {224 H 1792.3 O	1278.6	82.9	828.0	2189.5 {243.3 H 1946.2 O	+173.2 {+19.24 H +153.76 O	
Carbon	315.5	12.6	14.5	248.6	275.7	—39.8	
Hydrogen	270.9 {46.9 224.0	2.75	2.17	—	4.92 243.3 } 248.22	—22.7 } —41.98 +19.3	Fat, 51 grammes. Water, 85.9 grammes. C 39.8 ,, — ,, H 5.85 ,, H 9.54 ,,
Oxygen	2712.9 {920.6 1792.3	13.71	7.19	663.10	684.00 1946.20 } 2630.2	—82.7 } —236.6 +153.9	O 5.35 ,, O 76.35 ,,
Nitrogen	19.47	17.35	2.12	—	19.47	0	Leaving 7.31 H, 1.0 O.
Ash	23.9	18.1	5.9	—	24.00	+0.1	
2. AT WORK.							Decrease in Body Weight. 49.0 grammes.
Total Weight	3883.6	1261.1	126.0	2545.5	3932.6	+49.0	
Water	2266.53 {251.83 H 2014.70 O	1194.2	94.1	1411.8	2700.1 {300.0 H 2400.1 O	+433.57 } +48.17 H +385.4 O	Loss of Proteid, 266 grams. Fat, 34.6 grammes.
Carbon	309.17	12.6	14.5	309.20	336.3	+27.13	C 0.138 grammes. C 26.99 ,,
Hydrogen	297.74 {45.91 251.83	2.75	2.17	—	4.92 300.00 } 304.92	+7.18 } —40.99 +48.17	H 0.0186 ,, H 3.98 ,, N 0.04 ,, O 3.63 ,,
Oxygen	3232.45 {1217.75 2014.70	14.74	7.19	824.50	846.43 2400.10 } 3246.53	+14.08 } —371.32 +385.4	O 0.06 ,, Leaving 3.1814 grammes Hydrogen, and
Nitrogen	19.49	17.41	2.12	—	19.53	+0.04	10.39 ,, Oxygen.
Ash	24.88	19.4	5.9	—	25.3	+0.42	

3. DIFFERENCE.

	Totals.		Water.		Carbon.		Hydrogen (in Water).		Hydrogen (not in Water).		Oxygen (in Water).		Oxygen (not in Water).		Nitrogen.		Ash.	
	Taken in	Excret'd	Taken in	Excret'd	Taken in	Excret'd	Taken in	Excret'd	Taken in	Excret'd	Taken in	Excret'd	Taken in	Excret'd	Taken in	Excret'd	Taken in	Excreted
Rest	3342.7	3197.3	2016.3	2189.5	315.5	275.7	224	243.3	46.9	4.92	1792.3	1946.2	920.6	684	19.47	19.47	23.9	24.0
Work	3883.6	3932.6	2266.53	2700.1	309.17	336.3	251.83	300.0	45.91	4.92	2014.7	2400.1	1217.75	846.43	19.49	19.53	24.88	25.3
Difference	+540.9	+735.3	+250.23	+510.6	—6.33	+60.6	+27.83	+56.7	—0.99	±0	+222.4	+453.9	+297.15	+162.43	+0.02	+0.06	+0.98	+1.3

	Total.	Water.	Carbon.	Hydrogen in Water.	Hydrogen not in Water.	Oxygen in Water.	Oxygen not in Water.	Nitrogen.	Ash.
Difference between Intake and Output in Rest	+145.4	—173.2	+39.8	—19.3	+41.98	—153.76	+236.6	0	—0.1
Do. do. do. do. Work	—49.0	—433.57	—27.13	—48.17	+40.99	—385.4	+371.32	—0.04	—0.42
Do. at Rest over at Work	+194.4	—260.37	+66.93	—28.87	+0.99	—231.64	—134.72	+0.04	+0.32

from the alimentary canal as a constituent of proteid derivatives, such as leucin and tyrosin, which are changed into urea in the liver.

3. Some of the proteids in the blood may break down and be excreted as urea without having previously formed part of the tissue-cells.

4. The chief site of the breaking up of proteids for the production of physical work is in muscular tissue. Other tissues probably can supply proteid to make up the loss in the muscles when the individual is in poor training.

Metabolism of Carbo-hydrates.—We may begin this subject by giving shortly the main points of Bernard's glycogenic theory. The carbo-hydrates taken in as food pass into the blood of the portal vein as dextrose; are carried to the liver, and in part, probably in chief part, are arrested in that organ, where they are stored up as glycogen in its cells. From the liver, again, the glycogen is gradually given out in the form of sugar in the intervals of digestion, as required for the needs of the organism.

The nature and properties of the individual carbo-hydrates have already been described, but the leading characteristics of glycogen and sugar may be repeated. Glycogen is a polysaccharide corresponding in the animal to starch in vegetables, while dextrose and lævulose are simple monosaccharides capable of diffusion and of easy solution.

Carbo-hydrate taken in the form of dextrose or lævulose may be immediately oxidised, yielding carbonic acid, or may be stored up as glycogen in the liver. We have no evidence that carbo-hydrate bodies can form proteids, and although a carbo-hydrate diet favours the deposition of fat in the body, it has not as yet been absolutely proved, though it is almost certain, that the one can be changed directly into the other. Carbo-hydrates may form one of the sources of the lactic acid found in muscles, which yields carbonic acid on further oxidation; but this view has not been confirmed by recent observations. Whatever form the carbo-hydrates acquire before ultimate oxidation to carbonic acid and water, there is no doubt of the fact that the liver has much to do with the regulation of their stay and distribution in the body. Thus the blood of the portal vein during digestion contains more sugar than that of the hepatic vein, especially after a meal rich in carbo-hydrates; while, on the other hand, in the

intervals between the active digestion of food, the blood of the hepatic vein contains more sugar—2 parts per 1000—than the blood in the portal vein, or than the general blood-stream, which contains on an average 1 to 1.5 per 1000. Minkowski found that sugar rapidly disappeared from the blood in the goose when the circulation through its liver had been arrested. The facts which go to prove that the sugar stored up in the liver is in the form of glycogen are as follows:—

1. Glycogen has been found in the livers of a large number of species of animals, including some invertebrates.

2. In mammals it is most abundant in those feeding principally on carbo-hydrates.

3. It is found, however, in the livers of the carnivora and in those of the omnivora when feeding on flesh exclusively.

4. The quantity of glycogen in the liver gradually disappears in a fasting animal.

5. Fat alone does not give rise to an increase in the quantity of glycogen stored in the liver, nor can it arrest the disappearance of glycogen if no other food be given.

6. During early fœtal life glycogen can be recovered from all the tissues; later on it becomes more and more localised in the liver, although even in adults it may be found elsewhere, as for instance in the muscles.

If a rabbit be killed after a large meal chiefly consisting of carbo-hydrates, a meal of carrots for example, its liver rapidly excised, cut into small pieces, and thrown into boiling water which has been slightly acidulated, no sugar can be found in the extract filtered off from the coagulated proteids, even after the pieces of liver have been rubbed up in a mortar and boiled again. In this extract, however, glycogen is present in large quantity. Again, if the liver of an animal, killed some time previously, be excised, and treated as before, the watery extract contains very little glycogen but a proportionately large amount of sugar (dextrose). We may infer from these two experiments that boiling the liver destroys the agent which converts the hepatic glycogen into dextrose. And further, that the agent may be an unformed ferment or the change be occasioned by a direct action of the liver cells. Boiling destroys the activity of both such agents. After a meal containing much carbo-hydrate, the liver cells may be actually seen under the microscope to be loaded with some substance which is either glycogen itself or a closely allied body. The liver is then

large, soft, and friable, while after starvation it is small and firmer, and under the microscope the cells may be found to be shrunken.

An interesting observation has been made upon the glycogen contained in the liver of the frog. In winter the frog hibernates and for months takes no food, and during this period the liver cells contain a considerable amount of a substance which responds to tests in the same way as glycogen, although in summer, when in full activity, little or none can be detected. At first sight this fact seems inconsistent with the theory that glycogen is stored up in the liver, to be gradually distributed to the body in the form of sugar in proportion to the needs of the organism. But the condition of the liver of a winter frog can be changed into that usually found in summer by merely warming the atmosphere in which it is placed. At 20 or 25° C. the glycogen soon disappears; while on cooling a frog in summer by artificial means, glycogen accumulates in that organ. The rationale of these phenomena appears to be similar to that which is thought to explain the storage by plants of their surplus starch. In the frog in winter metabolism is slow, and some substance akin to sugar may be produced in the body in greater quantity than can be used up. The surplus is stored in the liver as glycogen, just as it is reserved by plants during autumn in the form of starch, for use in the coming spring.

If an animal be made to do severe muscular work while fasting, the glycogen rapidly disappears from its liver. If fasting, but kept at rest, the glycogen takes a longer time to leave the liver. In fasting animals there may not be a trace of glycogen left in the liver or the muscles, although there is still an abundance of fat in the body. From these facts we may argue that the glycogen stored in the liver and present in the muscles forms the readiest and most easily accessible source of energy for the organism. Carbo-hydrates can be utilised at once, fats require a longer time, while proteids are not utilised for some time further. As Stewart ingeniously puts it, glycogen resembles consols which can be realised at once, fats are like a good security but which requires some time for realisation, while tissue proteids are "long-date bills which can be only discounted sparingly and almost with a grudge."

An interesting question arises in connection with this subject. Where is the seat of the lesion in diabetes mellitus? We have seen that the

blood contains normally from 1 to 1.5 parts per thousand of sugar, much of which is used up during its circulation in the body, but a trace of which appears in the urine. One theory of the causation of diabetes mellitus ascribes it to the inability of the liver to store up carbo-hydrates in the form of glycogen, or to its too rapid distribution of the glycogen as sugar. It has been shown experimentally that any increase over the normal proportion of sugar in the blood at once causes its appearance in the urine. If the liver fails to regulate the passage of sugar into the blood-stream the symptoms of diabetes must necessarily follow. Observations which have been lately made upon the occurrence of this disease after excision of the pancreas or following disease of that organ, have suggested to some the presence of a ferment produced by the pancreatic cells which is able to convert sugars into glycogen. If this ferment be not produced owing to removal or to disease of the pancreas, the sugar absorbed after digestion will pass straight into the general blood-stream and at once be excreted by the kidneys. It would be a mistake, however, to ascribe all the causes of diabetes to the liver alone. In all its functions the liver is influenced by the conditions of other parts of the body, especially of the nervous system, and, although it is certain that in many instances the liver has much to do with its causation, in others the disease may be due to very diverse causes.

Although much of the hepatic glycogen is converted into sugar, we have no proof that the whole of it is so changed. Oil globules can often be seen in the liver-cells side by side with glycogen, and we know that fat may be formed from carbo-hydrates. Glycogen may then in part be a half-way house between sugar and fat. Proteids, however, are able to produce glycogen, so that as glycogen can be formed from proteid and fat from glycogen, glycogen may also act as an intermediary in the production of fat from proteid bodies.

Pavy has sought to prove that the glycogen stored up in the liver is never reconverted into sugar in health, but becomes other substances, such as fat and proteid; the sugar in the urine of diabetics arising from splitting of proteid molecules. But although he has expanded this theory with a wealth of illustration and many ingenious arguments, he has few supporters, and the doctrine of Bernard, stated shortly above, is that accepted by most modern observers. The fate of the sugar circulating in the blood appears to consist in its oxidation during the metabolism of the tissues into carbonic acid, which passes off in the venous blood. Some of it may be transformed into fat, but only a small proportion.

The recent results of Chauveau, from direct analysis of the blood before and after its passage through the muscles of the upper jaw of the horse during activity—*i.e.*, while chewing—serve to show that 3.5 times as much grape-sugar is oxidised by the active muscle as in the same muscle at rest. That is to say, that the amount of sugar in the blood coming from these

muscles is less than in the blood supplied to them, while the decrease of grape-sugar corresponds with the loss of oxygen in the blood entering the muscle, and the increase of carbonic acid in the blood which has passed through it. So, also, more grape-sugar is destroyed in the parotid gland of the horse when active than in a passive condition. In the gland, however, the proportion of sugar oxidised is far below that in a muscle of corresponding size.

The fact that the diabetes caused in an animal by puncture of the medulla oblongata at or near the region of the vaso-motor centre does not occur if the animal has been starved beforehand, when little or no glycogen is stored up in the liver, or if the splanchnic nerves, or the spinal cord above the third or fourth dorsal vertebra, be previously cut, shows: first, that the presence of an excess of carbo-hydrate is necessary, and, secondly, that nervous influences are involved. A substance called phloridzin, when given to an animal, produces diabetes, differing from that caused by puncture of the medulla, in that it can occur in an animal free from glycogen. In diabetes caused by this substance proteids are extensively destroyed. Another point which may be mentioned is that lævulose may be entirely used up in the tissues of a diabetic patient and cause no increase of sugar in the renal excretion, while dextrose, which is so similar to it, appears at once in the urine.

We may sum up the facts regarding the metabolism of carbohydrate substances in the body as follows:—

1. They are absorbed by the mucous membrane of the alimentary canal in the form of dextrose or grape-sugar.

2. The dextrose is carried by the portal vessels to the liver, where the excess not required to sustain the normal proportion of sugar in the blood is stored up in the liver cells in the form of glycogen.

3. In turn, part of the glycogen is re-converted into grape-sugar corresponding to the calls upon the blood for carbohydrate material by the tissues of the body, and is then distributed to all parts of the organism.

4. In the tissues it serves as a source of energy and of heat, owing to its oxidation and conversion into water and carbonic acid.

5. The carbonic acid resulting from this decomposition is carried by the pigment of the corpuscles in the venous blood to the lungs, and there exhaled.

6. Some of the grape-sugar may also be converted into fat in the liver.

7. Carbo-hydrates are never a source of proteid bodies.

The Metabolism of Fat.—The fat absorbed through the mucous membrane of the intestine passes along the thoracic duct and is thus conveyed directly into the blood-stream without passing beforehand, like the carbo-hydrates, through the liver. Normal blood, however, contains only the merest traces of fat save during active digestion, so that fats must be rapidly removed from the circulation in some part or other of the body. As fat contains a large proportion of carbon, it is clear that it is capable of serving as a powerful source of energy. It was at one time thought that the fat absorbed from the food was stored up in the fat-cells of adipose tissue, just as glycogen is in the liver, and given off as required for the needs of the body. But it appears probable that most of the fat taken is rapidly burned up and oxidised into carbonic acid and water, although any excess may be stored up in the form of adipose tissue. The question of the fate of the fats in the body is rendered difficult by the fact that fat may be produced both from carbo-hydrates and from proteids in the body. A cow will produce more fat in her milk than can be accounted for by that contained in her food. A bitch fed on lean meat may gain weight owing to the deposition of fat in its body, and even gain in weight by the deposition of fat while suckling her young. Analysis of the fat contained in the food of pigs has shown that it may only bear the proportion of 100 to each 472 parts of fat deposited in its body. So, again, bees can construct the wax of their cells from proteids, or use other substances for the purpose, such as sealing-wax. The fat of one animal differs in properties and in composition from that of another, and under ordinary circumstances retains its peculiar characteristics whatever the food may be or in whatever form fat itself may be given. The fat of a dog consists of a mixture of palmatin, olein, and stearin. If a dog be starved for some time and then given lean meat and a fat containing no stearin, the fat accumulated in the body is still composed of all the three principles. The stearin which must thus be formed may be either derived from the palmatin or olein in the food, or, and this is more likely, may be formed directly from the proteids of the food or of the tissues. It has been found that in such animals as the porpoise the fat deposited underneath the skin and forming the blubber has a different melting-point from that situated around the internal organs. There is no doubt that the fat stored up in the body is not the result of

the simple deposition of fats taken in with the food, but the outcome of complex chemical changes within the body. These changes result in the deposition of different fats characteristic of particular animals, or varying as to the part of the body in which they are located.

Urea contains 46 per cent. of nitrogen and 20 per cent. of carbon. The dry proteids from which it is derived only contain on an average 15 per cent. of nitrogen and 50 per cent. of carbon. That is to say, when the nitrogen of proteids has been completely eliminated in the form of urea only one-seventh of the carbon is got rid of by the same means. The carbon which remains is, under certain circumstances, stored up as fat.

To illustrate this point we may refer to an experiment of Pettenkofer and Voit on a dog excreting as much nitrogen as it was taking in its food. Two thousand grammes of lean meat were given each day. The nitrogen equilibrium remained constant, while 17 per cent. of the carbon of the food remained behind, representing about 58 grammes of fat. Again, as the administration of phosphorus causes the well-known fatty degeneration of many of the tissues of the body owing to decomposition of their proteids, so phloridzin hastens the disintegration of proteids, and, besides causing the appearance of sugar in the urine, produces an accumulation of fat within the cells.

It is a fact of great practical importance that an animal during lactation requires more proteid in its food than is necessary for the ordinary proteid metabolism of the body. Common experience has already taught all races the truth of this statement. The increase called for is rendered necessary by the large quantity of proteid bodies broken up in the formation of the fat secreted in the milk. The possibility of the arrest of a nitrogen-free portion of the albumin molecule in the form of glycogen or of fat is of great importance for the economy of the organism. Glycogen and fat thus produced serve as albumin-sparing bodies.

Fats also seem to be formed in the body from the carbo-hydrates present in it. It has been found that if proteids are added to a diet of carbo-hydrates in greater quantity than is necessary for nitrogenous equilibrium, fat is stored up. If the amount of proteid given be just sufficient to sustain the nitrogenous equilibrium, much less fat is produced. From this we can argue that the giving of carbo-hydrates for fattening purposes is based on the part taken by them in replacing

proteids and fats in the ordinary metabolic processes, acting, in fact, as a more ready source of energy, and allowing body fat to be stored up from the other two food elements. Voit has denied that fat is ever formed directly from carbohydrates, but Rubner has shown that if a dog is fed on an almost purely carbo-hydrate diet, containing a little fat but no proteid, the carbon excreted is less than can be ascribed to the destruction of proteids in the body or to the fat of the food.

Schulz's observations on the proportion of fat in the blood of normal and fasting animals are of great interest. According to his results, the blood of fasting animals—he used rabbits and pigeons—contains very much more fat than the blood of animals on a full diet. The excess in the rabbit may rise from 50 to 83 per cent., and in the pigeon from 30 to 100 per cent. This observation points to the abstraction during hunger of the elements of fat, or of fat itself, from the cells of the tissues and organs of the body rather than from the larger deposits of fatty tissue. Incidentally Schulz found that the percentage of fat in the blood of different animals varies to a remarkable extent. The blood of pigeons contains double the amount of fat present in the rabbit's blood.

Kaufmann, one of the most recent observers on the origin of fat in the body, contradicts Voit's dictum that the proteids of the food are the sole source of the fat formed, and regards the other food-stuffs as capable of supplying the necessary elements. If during digestion a large quantity of proteid is absorbed, much of it breaks down rapidly and forms fat. He states that the fat arising from chemical changes in the food-stuffs is employed in three ways. A part is oxidised, forms glucose, and supplies energy by its further combustion. A part is oxidised, but less completely, forming glycogen, which is stored up in the body. The remainder is deposited in the tissues as fat. When the amount of glycogen in the body is large the fat produced from the food is chiefly burnt off, or remains as fat in the tissues. If the body is poor in glycogen nearly all the fat not burnt off at once may be transformed into that carbo-hydrate. During the decomposition of albumin in the absence of free oxygen, with the production of fat and other bodies, it is probable that no heat is produced.

We may summarise the preceding paragraphs dealing with the metabolic processes in the body by stating that the three great groups of organic substances in the diet—proteids, carbohydrates, and fats—do not directly enter in an unaltered state into the composition of the tissues. The proteids may form in the organism similar proteid substances, and they may when undergoing destruction be so split up as to yield either carbohydrates or fats. The fats of the body may be derived, probably after intimate chemical decomposition and reconstruction, from the fat present in the food, or they may be formed in the body from proteids and from carbo-hydrates. The carbo-hydrates of the body may be derived from the

carbo-hydrates of the food or may be split off from proteids. It is probable that they cannot be produced from fat. Neither fats nor carbo-hydrates can form proteid substances in the body, but act as proteid-sparers, shielding them from a too rapid metabolism. Perhaps we might suggest as an illustration of the use of these three classes of food-stuffs in the body the simple one of an ordinary fire in any of our dwelling-houses. The carbo-hydrates might be likened to the paper, which is readily consumed; the fats to the wood, which requires a little longer and gives off more heat in combustion; while the coal might represent the proteid molecules, which contain a large store of potential energy, and are burned up more slowly than the others, but afford heat and energy for a much longer time. Such an illustration can only be applied to the physical aspect of the subject; chemically there is no relationship between the three fuels and the contrasted food-stuffs as regards the carbon available for combustion.

Salts.—A certain quantity of inorganic salts is required for the proper maintenance of the bodily functions. Each day about 30 grammes of inorganic salts are necessary. The practice of taking common salt with the food is largely due to the desire for a condiment, as the food itself contains sufficient or almost sufficient for the bodily needs. Bunge has shown, however, that the proportion of potassium to the sodium salts in the food exercises some influence on the quantity of common salt required. In flesh, the proportion of potassium to sodium is exactly that required, but in most vegetables the proportion is much too great. This excess of potassium salts in vegetable foods explains why vegetable-feeding animals and vegetarians wish for and require greater quantities of sodium chloride than meat-eaters. Should the salts be removed from the food as far as possible, and such salt-free food given to an animal, in a short time it becomes unhealthy, and in time, if salts are not added, death ensues. Organic salts appear also to be necessary for health, but to a much less extent. If the food for a long time contain no organic acids or salts, such as citric or tartaric acids, and the salts formed by these acids, the blood becomes changed in character and quality, while symptoms of scurvy may appear. One per cent. of common salt is sufficient to arrest gastric digestion, while one-half per cent. retards it markedly. The salts of the organic acids have a slightly greater retarding effect.

Von Liebig enunciated the "law of the minimum" in relation

to vegetable metabolism. This law is to the effect that a plant is unable to make use of a soil of the richest nutritious value unless a certain minimum quantity of mineral salts is available. This law holds good also for the animal organism. An animal deprived of all mineral salts in its food *dies as quickly as when starved.* Lunin fed mice on ash-free cheese and cane-sugar, with distilled water. The mice died in from 11 to 21 days. When common salt only was added to their food they lived for about the same length of time. Dried milk and distilled water sufficed to support mice indefinitely, but ash-free cheese and sugar mixed with inorganic salts in the same proportion to, and in the same relation with, the usual constituents of the ash of albumin, did not prevent death ensuing from the 20th to the 31st day.

The remarkable result of the last experiment can only be explained by the supposition that inorganic salts in an absolutely pure condition are unable to take the place of the same salts when intimately combined with proteid in the proteid molecule. The probability of such a suggestion is rendered greater by the analogous contrasts between the pharmacological actions of some natural and artificial drugs, apparently identical in composition, on the physiological processes of the body in health.

It is a peculiar circumstance that *post-mortem*, no change, or one which is barely perceptible and doubtful, can be demonstrated in the proportion of mineral salts contained in the organs of an animal which has died from the effects of "salts-hunger," from that obtaining in the organs of an animal given a full allowance of salts. Lime-salts are indispensable. If withheld the bones become altered, and symptoms of rickets appear.

The Ingestion and Metabolism of Iron.—Bunge found 0.047 grammes of iron per kilogramme in the body of a cat, and, calculating from this figure, the body of a man of 70 kilogrammes should contain .32 grammes. Stockman (*Journ. of Phys.*, 1895) has shown that the amount of iron ingested each day in an ordinary dietary only amounts to about 6 to 11 milligrammes ($\frac{1}{11}$ to $\frac{1}{6}$ grain), while the daily loss closely corresponds to these figures. As the intake is so small a reserve store of iron is rendered necessary for the organism to guard against emergencies, hæmorrhages, excessive destruction of red blood corpuscles from any cause, etc. This store is provided by the liver, whose cells rapidly take up any excess of the metal. Quite one-half the amount of an inorganic iron salt injected into the blood is detained by the hepatic cells. Zaleski and Vay showed that the iron arrested by the liver combined with various organic bodies in the cells,

a part in a much looser state than others. A part combines with the nucleo-albumins, and can only be separated from them by incineration; another portion forms as it were a "floating" (Stockman) store, more easily separated from its compounds, and therefore more available for the needs of the organism.

The iron set free by the breaking down of red blood corpuscles is in all probability stored up in the liver and not excreted, at least the greater part is thus detained. The actual iron metabolism must be very small, less than 10 milligrammes per day. Bunge has shown that artificial peptic digestion of the yolk of eggs yields an indigestible nuclein containing iron, all the other portions of the yolk being iron-free. As the yolk contains no hæmoglobin, and as during incubation no iron can enter from without, the iron-holding nuclein must afford the iron for the hæmoglobin of the chick. This nuclein he calls hæmatogen.

TABLE LVIII.

Hæmatogen. Per cent.		Hæmoglobin in the Hen. Per cent.
C 42.11	...	C 51.15
H 6.08	...	H 6.76
N 14.73	...	N 17.94
O 31.05	...	O 23.425
S 0.55	...	S 0.389
P 5.19	...	Fe 0.336
Fe 0.29		

If the molecular arrangement of these two substances be worked out,

$$\text{Hæmatogen} = C_{677}\,H_{1174}\,N_{206}\,O_{374}\,P_{32}\,Fe\,S_3 = 19{,}310$$
$$\text{Hæmoglobin} = C_{712}\,H_{1130}\,N_{214}\,O_{245}\,Fe\,S_2 = 16{,}710$$

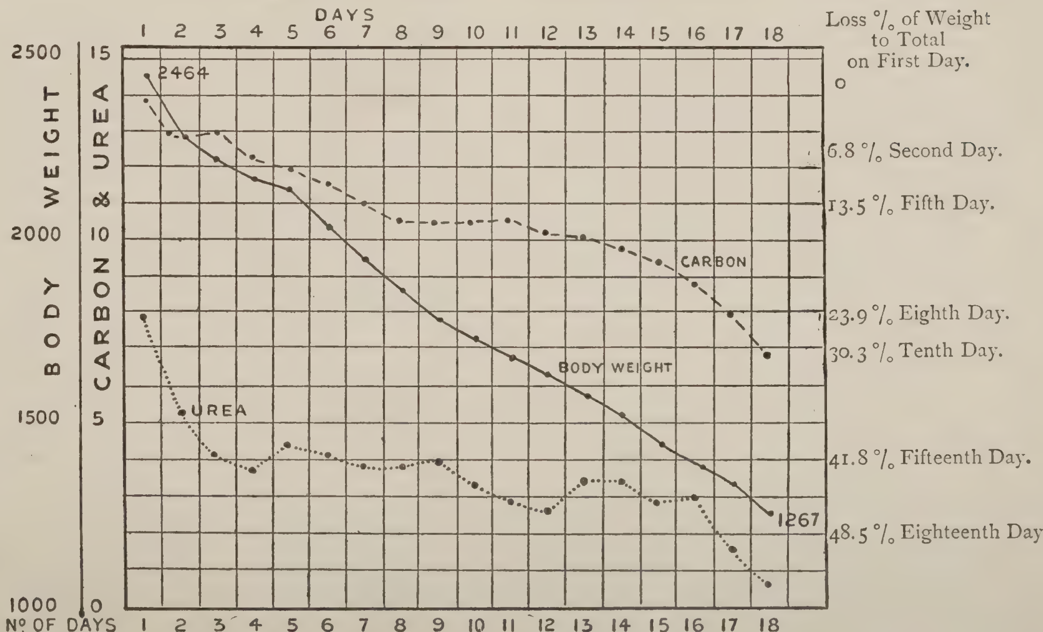
in molecular weight. While if the phosphorus in the hæmatogen be removed in the form of 32 molecules of phosphoric acid (H_3PO_4), the percentage of iron in the remainder closely corresponds to that found in hæmoglobin. The figures obtained do not tally exactly, the weight of the remainder being 16,174 instead of 16,710, but the hæmatogen analysed by Bunge was of doubtful purity.

Subtracting again the molecule of hæmatin from one of hæmoglobin, we obtain that of albumin.

$$\begin{array}{llr} \text{Hæmoglobin} & C_{712}\,H_{1130}\,N_{214}\,O_{245}\,Fe\,S_2 & = 16{,}710 \\ \text{Hæmatin} & -\ C_{32}\,H_{32}\,N_4\,O_4\,Fe & = 592 \\ \hline \text{Albumin} & -\ C_{680}\,H_{1098}\,N_{210}\,O_{241}\,S_2 & = 16{,}118 \end{array}$$

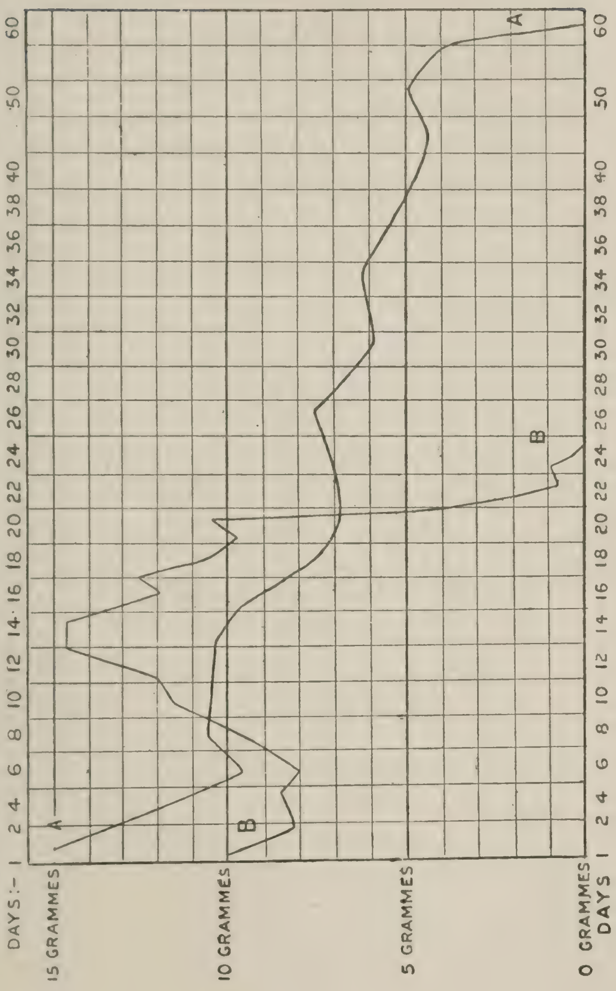
From these data we can understand how the organism has no need of much iron, important though the presence of the metal is for oxygenation in the blood and tissues. The iron absorbed is combined as hæmatogen or hæmoglobin, the excess is to a certain extent laid up as hæmatogen, the remainder is excreted. Frequently the fæces contain more iron than is represented by the food taken, owing to its excretion into the intestinal canal by the lining epithelium, which has been known for some time past to possess this power. Very little is

CHART XIV.—Graphic Representation of the Daily Loss of Carbonic Acid and Urea, and of the Decline in Weight of a Starving Cat. (Bidder and Schmidt.) In grammes.



The curve for the body weight shows the decrease in grammes each day, the figures on the right give in percentage values the proportion of loss on six of the days as compared with the original weight.

CHART XV.—Graphic Representation of the Daily Loss of Urea (A) in a Fat Dog starved for 60 days, and (B) in a Lean Dog starved for 24 days. (Constructed from data by Falck.)



excreted in the bile. It is a remarkable fact, and one which has led to much controversy of late years, that although the necessary amount of iron for the maintenance of health is absorbed from *organic compounds*, when given for disease arising from a poor state of the blood relatively large doses of *inorganic iron salts* are followed by better results than the administration of iron in organic combinations. Why this should be is doubtful. Injection of non-irritating organic iron compounds into the blood of anæmic persons is followed by rapid improvement. Bunge has suggested that the inorganic salts combine with sulphuretted hydrogen in the intestine, and forming the insoluble sulphide, are not absorbed but allow the organic compounds a better chance of gaining an entrance into the blood unchanged. But Stockman has shown that the sulphide of iron itself causes an increase of hæmoglobin in the blood of patients given it.

An observation by Socin has an important bearing on the question. He found that mice not only survived but had gained in weight at the end of 100 days during which they were fed on iron-free food.

In the normal course of events *only a small intake of iron is necessary* both for vegetable and animal organisms; the quantity excreted if no iron be taken in the food is small; the reserve of the metal in the form of hæmatogen is relatively large. States of anæmia, or poorness of blood, seem to arise either from long-continued insufficiency of the supply of iron salts, from constant, though often small, losses of blood, or from inability of the individual, owing to continued lack of iron in the food, to make use of organic iron supplied in small or moderate amounts, while able to benefit from the administration of large quantities of soluble inorganic compounds of that metal.

Metabolism during Starvation.—During starvation *the output is greater than the intake.* If the carbon and nitrogen excreted by a starving animal be estimated day by day diminishing amounts of each element can be recovered from the excretions as time advances. As there is no intake, the loss of each element continues to be proportional throughout the period of starvation to the available store in the body, until a time is reached when the processes necessary for the maintenance of life can no longer be supported by the elements left, and the death of the animal ensues.

A starving animal fulfils one of the common laws of nature, it makes the most of the material at hand. It spins out the inevitable loss as far as possible, indeed those substances which are absolutely essential for the preservation of the vital spark, or for the continuance of the action of such necessary organs as the heart and central nervous system, are only used up when the supply from other organs has almost entirely failed. Fats and any store of glycogen are first used up, along with part of the proteid, until, when from a quarter to a half of the total body weight has been lost, the machine stops for want of motive power.

Chart XIV., representing the actual loss in grammes of body weight and of carbon and urea in a fasting cat, as estimated by Bidder and Schmidt, shows the daily variations in the values of each factor. The amount of urea does not diminish during the first twenty-four hours, owing to excretion of the nitrogen contained in the food last taken. Indeed, if the animal be of lean habit the proportion of urea excreted rises during the first few days because of the increased consumption of proteid in the absence of fat (Chart XV.). When depositions of fat are present the daily loss of fat is nearly constant, but however much be stored up in the tissues some proteid waste must occur to allow the vital processes to continue. The fat only serves as a proteid-sparer economising the necessary use of the nitrogenous substances.

As has already been mentioned, the loss is not borne by all the organs alike. Generally stated, we may say that the less important an organ or tissue is for the preservation of life the greater is its waste during starvation. Diagrams IV. and V. have been constructed from data given by Voit as to the loss of weight in the individual organs and tissues after death from starvation. The proportion which the loss in each bears to the weight of a similar animal killed when in good condition is also included in it.

From these figures it appears that although the waste of the muscular tissue of the body forms the largest part of the total loss of weight, it only reaches 31 per cent. of the total muscular substance, while, though the actual proportion of weight lost is less, 97 per cent. of the fat present is used up. The other organs which lose much of their weight are the spleen with 67 per cent., the liver with 54 per cent., and the testes with 40 per cent. The central nervous tissue and the heart only

DIAGRAM IV.—Showing the Loss of Weight of the various Organs after Death from Starvation.

I.—Percentage of Total Loss borne by each Organ.

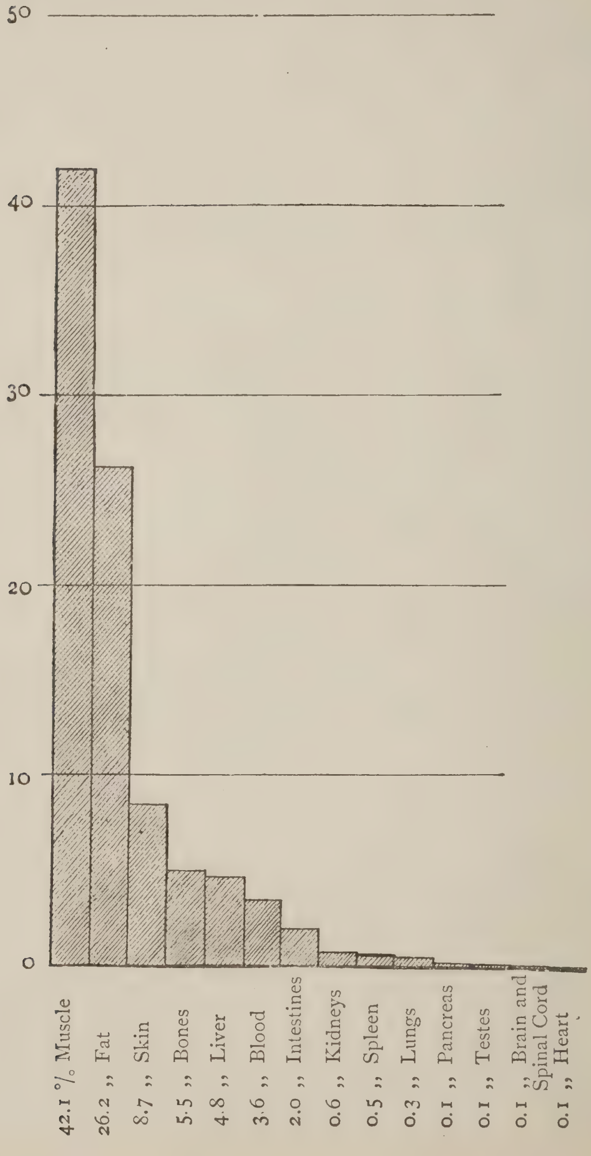


DIAGRAM V.—Showing the Loss of Weight of the various Organs after Death from Starvation.

II.—Percentage Loss in each Organ.

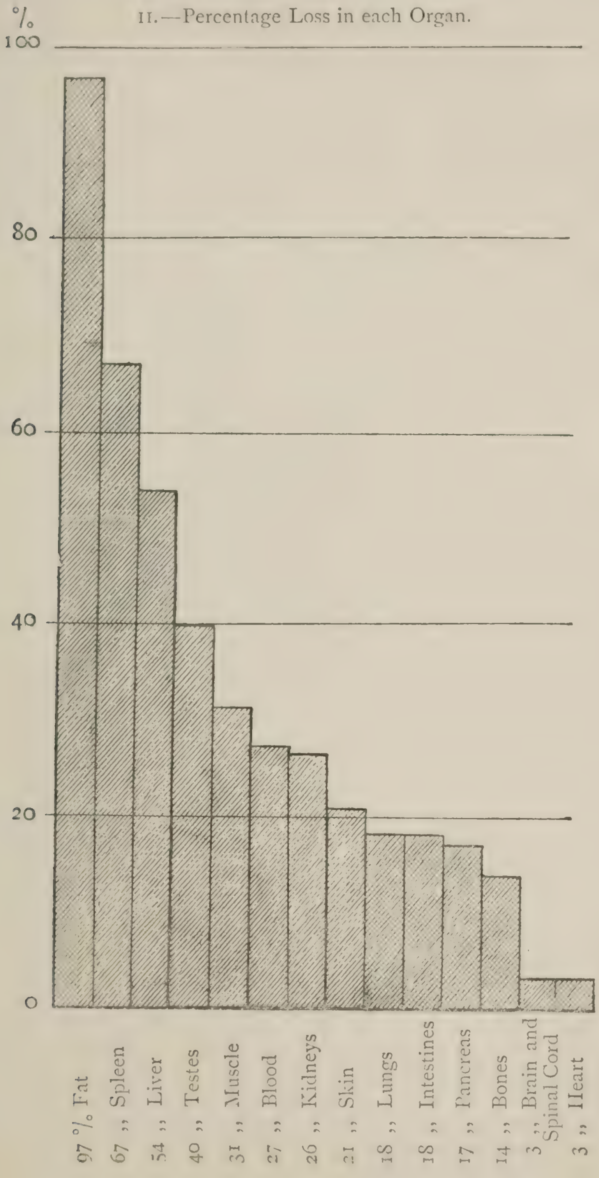


TABLE LIX.—*The Daily Changes in a Dog of 35 kilogrammes when starved and then fed with Increasing Amounts of Lean Meat.* (*After Voit.*)

Day.	Intake.			Output.					Total N.	Total C.	Difference.
	Food.	N.	C.	Urea.			Carbonic Acid.				
				Total.	N.	C.	CO_2.	C.			
I.	0	0	0	10.7	5	2	110	30	5	32	− 5 grms. N, − 20 grms. C } = 150 grms. Flesh. − 12 grms. C = 16 grms. Fat. Loss in weight, 166 grms.
II.	Meat—150 grms.	5	20	15	7	3	143	39	7	42	− 2 grms. N, − 8 grms. C } = 60 grms. Flesh. − 14 grms. C = 18 grms. Fat. Loss in weight, 78 grms.
III.	,, 500 ,,	16.6	66.6	35.6	16.6	7	220	60	16.6	67	± 0 grms. N. No loss of flesh. ± 0 grms. C. No loss of fat. Weight constant.
IV.	,, 1000 ,,	32	133	70	33	14	275	75	33	89	± 0 grms. N. No loss of flesh. + 44 grms. C, or 59 grms. of Fat. Gain in weight, 59 grms.

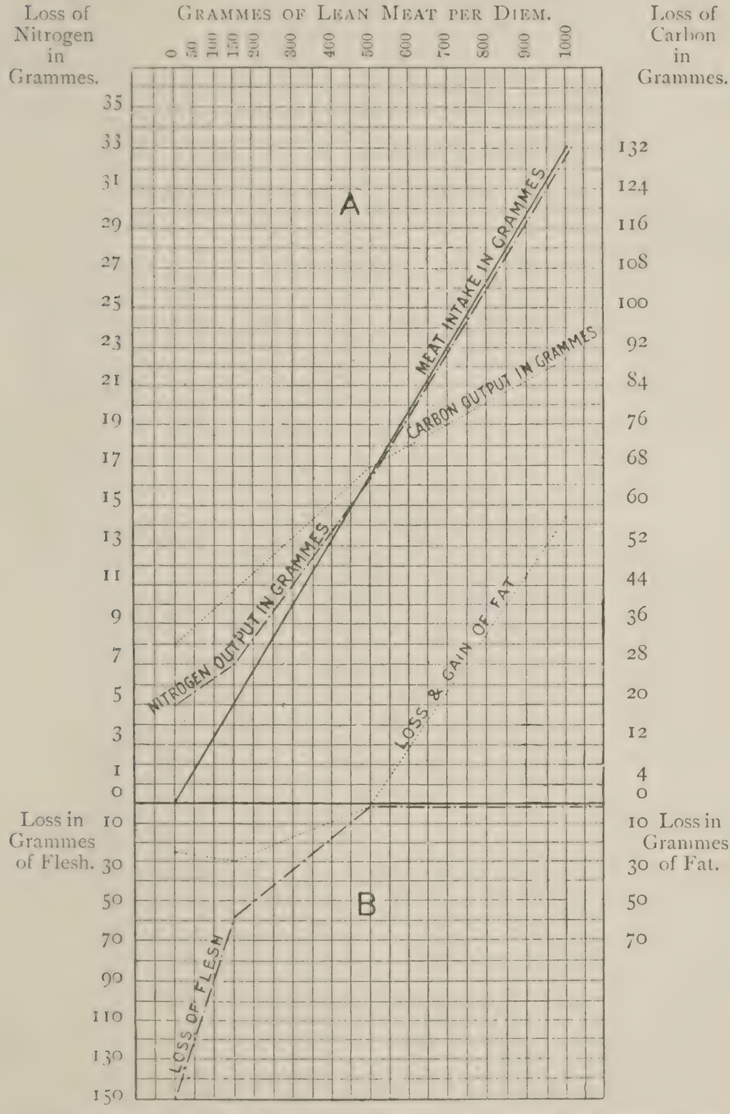
A fasting dog of 10 kilos produces about 500 kilocalories of heat per diem.
1 gramme of meat produces 1 kilocalorie, 1 gramme of fat about 9 kilocalories.

Day.	Calories Taken.	Equivalent Calories of Excretion.
I.	0 - - - -	150 grammes Flesh = 150 kilocalories, 16 grammes Fat = 144 kilocalories = − 294.
II.	150 kilocalories - -	210 ,, ,, = 210 ,, 18 ,, ,, = 162 ,, = − 222.
III.	500 ,, - -	500 ,, ,, = 500 ,, 0 ,, ,, = 0 ,, = + 0.
IV.	1000 ,, - -	1000 ,, ,, = 1000 ,, 59 ,, ,, = 531 ,, = + 469.

N = Nitrogen. C = Carbon. CO_2 = Carbonic Acid.

For the first three days the loss in flesh as represented by the amount of nitrogen excreted, and in fat represented by the excess of carbon excreted above the proportion contained in the amount of flesh lost, are shown in the lower section in calories. For the fourth day the loss of flesh equals the intake of nitrogen, and the excess of carbon remaining as fat represents calories of heat which must be taken from those of the proportional amount of heat.

CHART XVI.—Showing the Loss in Flesh and Fat of a Dog of 10 Kilogrammes, fed on Lean Meat alone, in increasing quantities. (After Voit.)



The amounts of flesh given read horizontally: those for nitrogen and flesh from the figures on the left, for carbon and fat from those on the right.

In the upper part, or A (the zero line indicating balance of intake and output), the food taken and the nitrogen and carbon lost are shown.

In B the loss or gain in flesh and fat are represented.

supply 0.1 per cent. of the total loss, and 3 per cent. of their actual substance.

Knowing the daily loss of nitrogen in a starving animal, it might be supposed that an equivalent amount of nitrogenous food given by the mouth would restore the nitrogenous equilibrium. This, however, is not the case. The exact amount of nitrogen given in the form of proteids is insufficient. Voit found that when a dog of 30 kilogrammes in weight, excreting daily 11.4 grammes of urea, on the tenth day of starvation was given an equivalent amount of dry proteid, about 34 grammes, the excretion of urea was almost doubled but still represented more nitrogen than that in the food. Progressive increase of the proteid given resulted in nitrogenous equilibrium being established, but only when the quantity ingested was far above that requisite to counterbalance the loss of nitrogen during starvation. Even when 480 grammes of flesh in the day was given the loss in body weight was 12 grammes. About 500 grammes would probably have adjusted the equilibrium, or nearly treble the quantity which represents 11.4 grammes of urea (see Table LIX.). (Chart XVI.)

CHAPTER XV.

Dietetics and Animal Heat.

The Ideal Physiological Diet:—Relation of Diet to Body Weight—Variations in Diet—Necessary Amounts of Oxygen and Hydrogen—Diet in Young Animals.
Animal Heat:—Amount—Source—Seat of Production.

The knowledge which we have obtained from the outline given in the last chapter of the main features of the metabolic processes in animals may now be applied to the consideration of the ideal physiological diet and to the many variations of it used by animals to attain the identical result—healthy existence and growth.

All animals derive their nourishment from the vegetable kingdom, either directly from it, or indirectly by living on other animals which in turn feed upon vegetable bodies. Throughout the animal kingdom there are immense differences in the diet of different species, or even in different individuals of a single species. The normal diet for an animal organism contains the three groups of food-stuffs mentioned above—proteids or nitrogenous substances, carbo-hydrates, and fats. Some animals live entirely upon vegetable products, others exclusively upon nitrogenous bodies, with the addition as a rule of fats, while in others, again, the diet contains all the three classes. There is no doubt that the processes of metabolism in the body can render very dissimilar diets of like service to the organism. The Eskimo living upon flesh and fat, the Chinese coolie living exclusively on rice, the Irishman with a staple diet of potatoes, or the inhabitant of Great Britain living on a mixed diet, do not differ very materially from one another as far as the ultimate constitution and chemical processes of the body are concerned. A cow on an exclusive diet of grass is able to form the same tissues from the same chemical elements

as the lion or tiger living on flesh. The dog apparently thrives equally well on a flesh diet or on one consisting principally of carbo-hydrates; the chemical constitution of its tissues, as far as we can investigate them, appears to be the same in either case, although certain differences, it must be allowed, do occur, especially with regard to nervous attributes, such as temperament and obedience. As a general rule, although the laws of metabolism work in similar ways whatever diet may be in question, one or two smaller points of difference can be detected between the carnivorous and the herbivorous animals. The flesh-eating animals are capable of more prolonged exertion, and, bulk for bulk, possess greater muscular activity and strength. They are not prone to lay on so much fat; their flesh has generally a strong and often unpleasant flavour, and their bodies in life a rank and generally disagreeable odour; and lastly, their temperament is very different. The great difference between a purely vegetable diet and one composed exclusively of animal tissue, although the general laws of metabolism hold good in both, must thus have some effect in the way of altering the constitution of the tissues to a greater degree than the small change in the metabolic processes can account for.

The ideal physiological diet is one which contains the requisite quantities of nitrogen, carbon, inorganic salts, and water to keep the organism in a state of equilibrium—that is, to render the intake of these substances equal to their output—in the smallest bulk possible, whereby no excess of any of them is taken in with the food. The output of the body varies with its size, its age, the amount of work done, the conditions of climate in which it exists, its personal surroundings, and the peculiarities of its alimentary canal and digestive apparatus. The true physiological diet which suffices to supply the needs of the body exactly, and which contains no surplus element, varies with each individual.

In dealing with this question it is manifestly impossible to formulate rules applicable to each individual case, and recourse must be had, as in almost all scientific inquiries concerning living things, to the law of averages. As the significance of dietetic rules is more easy of comprehension when relating to human beings than when applied to other animals, the chief part of this section is devoted to the consideration of the diet of man. Of course experiments impossible in man

TABLE LX.—*Classification of Food Principles.*

Class.			Products of Digestion.		Products of Metabolism.	
Proteids: C 53.5% H 7% N 15–16% O 22% S 2%	Albumins: N : C : : 2 : 7	Serum albumin Egg albumin Serum globulin Egg globulin Fibrin Myosin Lact-albumin Plant albumin Vitellin, phytovitellin Coagulated proteid Hæmoglobin	1. *Proteids.* Acid-albumin Alkali-albumin Hetero-albumose Dys-albumose Proto-albumose Deutero-albumose Peptone	2. *Decomposition.* Leucin Tyrosin Lysin Lysatinin Ammonia Tryptophan Aspartic acid Indol, etc.	1. *When used.* 1. Tissue and circulating proteid 2. Fat 3. Carbo-hydrate	2. *When excreted.* Sulphuric acid Urea Water Carbonic acid (C20%, N46.6%, N : C : : 2.3 : 1)
		Gelatin	Gelatoses	Glycocoll, etc.	Tissue and circulating proteid, $\frac{5}{6}$ value of last group	Urea
	Albuminoids: N : C : : 2 : $5\frac{1}{2}$	Keratin Chondrin	Keratoses, etc. Peptone		Fat Carbo-hydrate	Water Carbonic acid
	Extractives: N : C : : 2 : 2.5 or 3	Kreatin Sarcosin Kreatinin	None	—	—	As taken in
Fats: C 77% H 12% O 11%		Palmitin Olein Stearin Lecithin				Carbonic acid and water
Carbo-hydrates: C 44.4% H 6.1% O 49.5%	Polysaccharides	Starch Dextrin Glycogen	Maltose Dextrose and lævulose	(saliva, pancreas) (intestinal ferment)	Glycogen Dextrose Fats by reduction Supply heat by oxidation	Carbonic acid and water
	Disaccharides	Sucrose Lactose Maltose	Maltose Dextrose and lævulose	(saliva, pancreas) (intestinal ferment)		
	Monosaccharides	Dextrose Lævulose Galactose	Lævulose Dextrose	(HCl in gastric juice)		

must be recorded and illustrative examples from the lower animals incidentally alluded to; but the subject of diet in animals is discussed in its relation to the general laws laid down for man in the sequel. (Table LX.)

In considering the normal diet of man most observers have calculated the necessary proportions of food-elements required to maintain bodily equilibrium in an adult of 70 kilogrammes—11 stones or 154 lb.—in weight. The average discharge of carbon and nitrogen from a man of this weight is 230 grammes and 15 grammes daily, provided he be healthy and performing little bodily labour; in addition 2250 c.c. of water and 24.0 grammes (Voit), and 30 grammes (Moleschott), or 25 grammes (Ranke) of inorganic salts are excreted. For the purpose of oxidising the carbon taken in in the form of food-stuffs, corresponding to the output given above, 85 litres of oxygen will be required. Theoretically, while a man of 70 kilogrammes remains in health and of constant weight, his diet need only contain the same number of grammes of carbon and nitrogen. But such a diet would leave no margin between the intake and output, and the normal diet should be calculated to contain 20 grammes of nitrogen and 300 grammes of carbon. If with this increased diet the weight still remains constant, the output rises in direct proportion; while, as the smaller amounts are sufficient to maintain the body-weight, the excess taken in is excreted practically as a waste product. If, however, any increase in the amounts of carbon and nitrogen over those contained in the minimum diet capable of maintaining a constant weight be given, and less carbon and nitrogen excreted than taken in, the body-weight will be found to be greater; and, conversely, should more carbon and nitrogen be given off than taken in in the food, the body-weight falls. The diminished output of carbon signifies an increase in the bodily fat, an increased output a loss of fat from the body. When less nitrogen is excreted than is taken in, the difference remains in the body as proteid, that is, flesh; when more nitrogen is lost than is taken, the body loses flesh. Knowing the quantities requisite, it is easy to calculate the amounts of actual food-stuffs which are able to furnish the nitrogen, carbon, salts, and water for the bodily metabolism. The following table represents the proportion of nitrogen, carbon, hydrogen, and oxygen in proteids, carbo-hydrates, and fats when free from water and salts:—

TABLE LXI.—*Composition of Food Elements.*

	Nitrogen, per cent.	Carbon, per cent.	Hydrogen, per cent.	Oxygen, per cent.	Amount required to give 20 grms. Nitrogen.	Amount required to give 300 grms. Carbon.	Nitrogen to Carbon as
Proteid -	15-16	50-53 ...	7 ...	21-22	140 grm....	600 grm...	1 to 3.3 or 3.53
Fat -	- — ...	77	... 12 ...	11 ...	—	... 389 grm...	—
Carbo-hydrate	— ...	44.4	... 6.1 ...	49.5 ...	—	... 680 grm...	—

The proper proportion between the nitrogen and the carbon in the food is 20 : 300, or 1 : 15. The figures given in the table show that a diet composed solely of proteids requires 140 grammes *per diem* to afford the necessary 20 grammes of nitrogen, while this amount would only yield 70 grammes towards the requisite 300 grammes of carbon. Rather more than four times that amount is necessary to provide 300 grammes of carbon, and therefore the necessary number of grammes of carbon can only be supplied in the form of pure proteid along with 90 grammes of nitrogen, or 4.5 times that which is wanted. Neither fats nor carbo-hydrates contain nitrogen, while 389 grammes of fat and 680 grammes of carbo-hydrates can supply the 300 grammes of carbon.

But few people either care to live on a physiologically correct diet, or can obtain the proper articles of food required to form it. Thus the Chinese labourer has to consume normally 2000 grammes of rice to obtain 20 grammes of nitrogen, and at the same time takes in 700 grammes of carbon, or twice as much as he requires. More work is, therefore, laid upon the tissues engaged in their metabolism than should be physiologically. The Irish peasant is situated in even a worse plight: to obtain his daily 20 grammes of nitrogen he has to consume 5 kilogrammes of potatoes, which contain nearly double the requisite 300 grammes of carbon. On the other hand, a man living on flesh alone would require 2400 grammes of meat to yield the necessary amount of carbon, although 600 grammes would be sufficient to yield the nitrogen required. Oatmeal and wheaten flour contain nitrogen and carbon in almost the normal proportions, 1 to 15; oatmeal contains a little more nitrogen than wheat flour. (Table LXII.)

TABLE LXII.—*Showing the Normal Metabolic Changes in the Nitrogen, Hydrogen, Carbon, Oxygen, and Salts of a Diet capable of maintaining Nitrogenous Equilibrium in an Adult. (In grammes.) The Diet containing of Proteid,* 140 *grammes; Fat,* 100 *grammes; Carbo-hydrate,* 350 *grammes.*

INTAKE.					OUTPUT.								
Elements of the Food ingested.	Total Weight of Foods.	Number of grammes of elements available. 1 In food.	2 Excreted in fæces unused.	3 Total available in body.	Kidney.	Lung.	Skin.	Other-wise.	Total.	Differ-ence from intake.	Addition to body equal to Fat.	Water.	Remaining Unaccounted for.
NITROGEN—													
Proteids	140 grms.	19.47	2.0	17.47	17.35	—	0.12	—	17.47	0	—	—	—
HYDROGEN—													
Proteid	140 ,,	9.8	2.17		2.75 solids.	—							
Fat	100 ,,	12.0											
Carbo-hydrate	350 ,,	21.6			142.06	36.8	55.3	—					
Water	2016.3 ,,	224.0	9.2		water.				236.91	−19.12	4.59	9.64	4.89
TOTAL		267.4	11.37	256.03	144.81	36.8	55.3						
CARBON—													
Proteid	140 ,,	75.0											
Fat	100 ,,	79.0	14.3		12.6	248.66	0.35	0.46					
Carbo-hydrate	350 ,,	155.4			solids.	as CO_2	as CO_2		262.07	−33.03	33.03	—	—
TOTAL		309.4	14.3	295.1	12.6	248.66	0.35	0.46					
OXYGEN—													
Proteid	140 ,,	29.4	7.19		13.71								
Fat	100 ,,	11.5			solids.	663.09	0.93	1.5					
Carbo-hydrate	350 ,,	172.8				as CO_2	as CO_3	as SO_3					
Water	2016.3 ,,	1792.0	73.7		1136.48	294.4	442.4		2552.51	−81.3	4.18	77.12	—
			O^2 expired.		water.	water.	water.	—					
Air	15000 litres	44662.0	43953										
TOTAL		46667.7	44033.89	2633.81	1150.19	957.49	443.33	1.5					
WATER—		2016.3	82.9	1933.4	1278.54	331.2	497.7	0	2107.44	+164.44	—	—	—
SALTS—		23.9	5.9	18.0	12.8	—	5.3	0	18.1	+0.1	—	—	—
										Total.	41.8	86.76	4.89

TOTALS—	Taken in	Unused. Fæces and air.	OUTPUT. Absorbed.	Kidney.	Lung.	Skin.	Other-wise.	Quantity of Oxygen necessary to oxidise the elements.	Oxygen present in food and available (in proteid).	Oxygen deficit or surplus.	Oxygen in water given.	Oxygen in air.
Nitrogen	19.47	2.0	17.47	17.35	—	0.12	—	13.71	22.21	+9.5	—	—
Hydrogen	267.4	11.37	256.03	144.81	36.8	55.3	—	1873.28	—			
Carbon	309.4	14.3	295.1	12.6	248.66	0.35	0.46	664.02 2537.3	—			
Oxygen	46667.7	44033.89	2633.81	1150.19	957.49	443.33	1.5	—	184.3	−2353.0	+1718.3	+709
Salts	23.9	5.9	18.0	12.8	—	5.3	—	—	—		Deficit.	Excess.
Total	47287.87	44067.46	3220.41	1337.75	1241.95	504.59	1.96	2551.01	206.51	−2343.5	−625.2	+83.8

A physiologically correct diet might be formed of 140 grammes of proteid, and either 515 grammes of starch, or 300 grammes of fat; but experience and experiment have shown that, for civilised man at least, a mixture of the two is conducive to, indeed is necessary for, health. Some races of men subsist for long periods almost entirely on flesh without apparent detriment to their nutrition; others, the Eskimo for instance, on meat and fat, and dogs remain in health on a diet of proteids and fats. To cite a well-known modern example, Nansen and his companion suffered little inconvenience from an enforced exclusion of carbo-hydrates from their food during the course of many months, or rather may be said to have benefited by it, as they put on weight while on a diet of meat and fat, notwithstanding the arduous nature of their enterprise. As a rule, however, it is more conducive to health if the carbon necessary, over and above that contained in the nitrogenous elements, be supplied partly as fat and partly as carbo-hydrate in the food. Should our man of normal weight be doing no work, he should be given at least 50 grammes of fat, or 37.5 grammes of carbon; but twice this quantity would be more beneficial, especially if he be engaged in moderate labour. One hundred grammes of fat yield about 75 grammes of carbon, and added to the 70 grammes contained in 140 grammes of proteid, leave 155 grammes of carbon to be taken in the form of a carbo-hydrate. This amount can be obtained from 350 grammes of starch. To these must be added 30 grammes of inorganic salts, and 2.25 to 2.75 litres of water. Comparing these figures with the body weight, we find the following :—

TABLE LXIII.—*Comparison of the necessary amounts of the Food Elements with the Weight of the Body.*

	Food Element.	Amount in Grammes.	Proportion to Body Weight.
1.	Proteids	140 ...	0.2 °/₀ or $\frac{1}{500}$
2.	Fat	100 ...	0.14 °/₀ or $\frac{1}{700}$
3.	Carbo-hydrates ...	350 ...	0.5 °/₀ or $\frac{1}{200}$
4.	Salts	30 ...	0.042 °/₀ or $\frac{1}{2333}$
5.	Water	2500 ...	3.6 °/₀ or $\frac{1}{28}$

To put it in another way, a sufficient diet for man will contain 2 grammes of proteid, 1.4 gramme of fat, 5 grammes of carbo-hydrate, and 0.4 gramme of salt to each kilogramme

of body weight, or *nearly* 1 *per cent. of solid food*, in which nitrogen bears the proportion to carbon of 1 to 15.

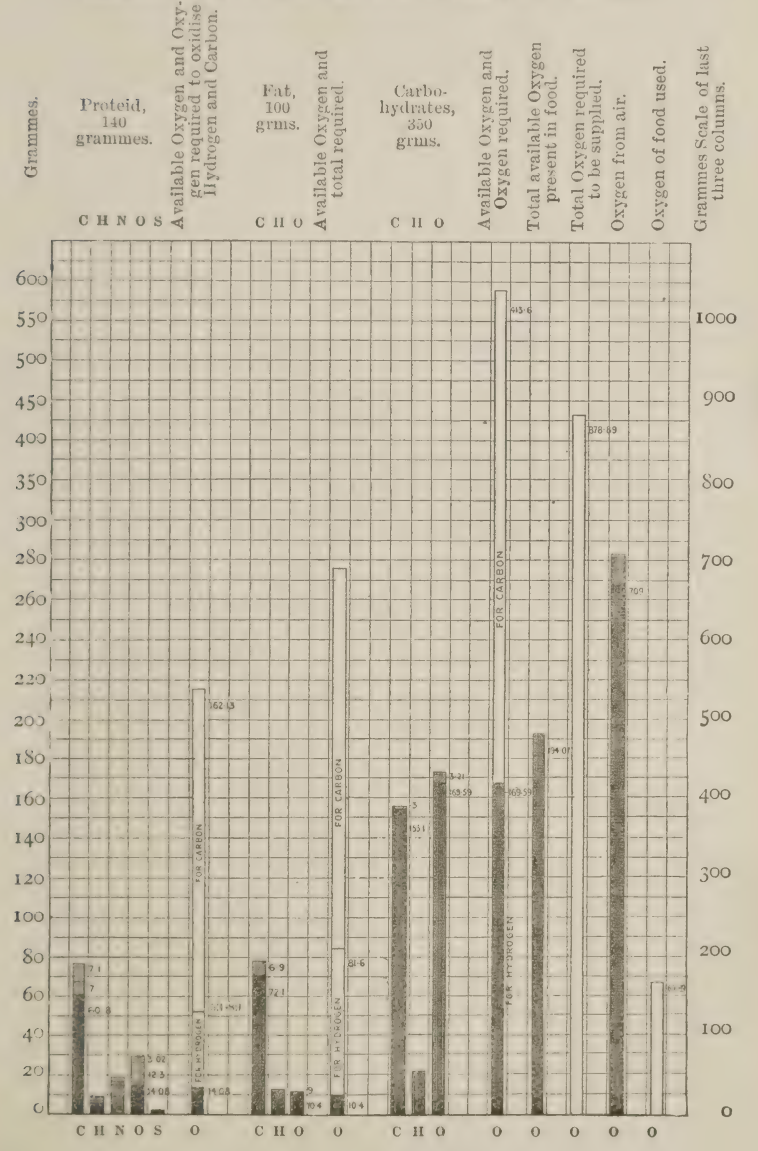
A cardinal point in all dietaries consists in the fact that the bodily processes cannot normally go on without the ingestion of a certain quantity of nitrogenous food. The proportion of fat and carbo-hydrates may be varied very considerably. Man can exist on a spare diet, provided he is not engaged on severe manual labour. An emaciated body can do little work, and requires less proteid. Playfair found, thirty years ago, that a London needlewoman lived on a daily regimen containing 54 grammes of proteid, 29 grammes of fat, and 292 grammes of carbo-hydrates. This must surely be the absolute minimum on which life can be supported. Indeed, Voit remarks that the Trappist monk, who practises the severest form of asceticism, consumes each day 38 grammes of proteid, 11 grammes of fat, and 469 grammes of carbo-hydrates.

Young animals, which have not reached their full growth or maturity, require more food than their weight would suggest. Their income must exceed their outgo to allow them to grow. Again, the outgo from the body is much more nearly proportional to the superficies than to the mass. As a rule, the cube of the surface of an animal varies directly as the square of the mass; when the weight becomes double, the surface therefore is only one and a half times greater than before. A boy of from six to nine years, and weighing 18 to 24 kilogrammes, presents an extent of skin two-fifths to one-half that of the adult weighing 70 kilogrammes. He requires about as much as one-half of the food of an adult. So Voit states than an infant of four months, weighing 5.3 kilogrammes, consumes in its daily food .6 gramme of nitrogen for each kilogramme of its body weight, compared with only .275 gramme of nitrogen per kilogramme in an adult of 71 kilogrammes.

The Requisite Amounts of Oxygen and Hydrogen.—As has already been stated in the consideration of general metabolism, the nitrogen leaves the body chiefly in the form of urea, or as uric acid in some animals, while the carbon is oxidised and passes off mainly as carbonic acid. The amount of oxygen taken in by the lungs is greater, however, than that which reappears in the form of carbonic acid. Some of it goes to oxidise other elements, and especially to act on hydrogen with the formation of water. (Diagram VI.—The amount of each element passed in the fæces is represented by diagonal shading, and in the

DIAGRAM VI.—Showing the actual amounts of Oxygen contained in the Three Principal Food Elements, and the amounts necessary for their full oxidation. The food contains 140 grammes of Proteid, 100 grammes of Fat, and 350 grammes of Carbo-hydrate material, and serves to maintain nitrogenous equilibrium. (For explanation see text, foot of page 328.)

C = Carbon. H = Hydrogen. N = Nitrogen. O = Oxygen. S = Sulphur.



urine by horizontal lines. The actual quantities oxidised in the body are given in vertical lines. The oxygen available in each class of food for oxidation is finally repeated in solid black, with the additional oxygen needed for complete oxidation of all the elements in white columns. The last three columns are drawn to a reduced scale, and denote in a similar manner the total oxygen required, the oxygen obtained from the inspired air, and the amount of oxygen from the food used up. The figures inserted in the body of the diagram indicate the amounts of oxygen required to oxidise the hydrogen and carbon of the food separately. Added together, *minus* the oxygen in the food, the sum corresponds to the scale. The figures throughout are in grammes.)

A more minute study of the question reveals several important facts. In the first place, the carbo-hydrates are bodies which contain the two elements hydrogen and oxygen in the proper proportion for the formation of water, and these elements may unite in the form of water in the body, leaving the carbon to unite with the oxygen in the blood. The changes here cannot account for any of the oxygen deficit. Secondly, the hydrogen of the fats is much more than can be completely oxidised by their oxygen. Hydrogen requires eight times its weight of oxygen to form water, while fat only contains about weight for weight of the two elements (12 : 11), so that 100 grammes of fat require about 80 grammes of oxygen to be supplied before all the hydrogen can be completely oxidised. In proteids, again, there are 15 grammes of nitrogen, 7 grammes of hydrogen, and 21 grammes of oxygen in each 100 grammes. Thirty-three grammes of urea correspond to 100 grammes of dry proteid, and contain 15 grammes of nitrogen; but the hydrogen in this quantity of urea is only about 2 grammes, the oxygen about 9 grammes; .5 grammes of hydrogen and 12 grammes of oxygen remain unaccounted for. Bearing in mind the proportion of oxygen required to oxidise hydrogen, it is clear that 40 grammes of oxygen are necessary to form water, of which only 12 grammes can be obtained from the proteid, leaving 28 grammes to be provided by the oxygen taken in in respiration. (Table LXIV.)

Alimentation with the antipeptone obtained from digestion of glandular tissues, especially that from the auto-digestion of the pancreas, has been found by Ellinger (*Zeit. f. Biol.*, xxxiii., p. 190) to be of less value in the preservation of nutrition than

an equivalent ingestion of albumin. The epithelium of the alimentary mucous membrane appears to be unable to transform all the peptone introduced into albumin during its absorption, and the unconverted part of the peptone acts in the blood as a toxic agent. Food elements taken in a less soluble form, or even when insoluble in water, are of greater nutritive value than the rapidly soluble substances.

Animal Heat.—The higher animals—mammals and birds—have, with a few exceptions, a practically constant internal body temperature. Such animals are termed homoiothermal. A few hibernating mammals, the marmot for instance, have a constant body temperature during the summer, but a varying temperature in winter during hibernation, when the temperature follows closely that of the environment. When the body temperature varies in this manner the animal is termed poikilothermal. In the lower forms the body temperature always varies with the surrounding degree of warmth, but is usually slightly above it. In a healthy man the internal body temperature remains constant at about 98° Fahr. (38° Cent.) under all conditions, and in a frog it may be 30° Cent. in summer and only 5° Cent. in January. In both the man and the frog, however, heat production is constantly going on, although, in relation to each unit of weight, the amount produced by the frog is much less than in the case of the man, and more easily lost. The tissues of the lower animals are unaffected by changes in the internal body temperature which would suffice to disorganise the tissues of the higher forms.

It is impossible to enter into all the details concerning animal heat in this book; only that part of the subject germane to the discussion of bodily metabolism will be described—that is to say, the rôle which the products of digestion play in the production of heat. All the heat produced in the body arises from the combustion of the food taken in. Relatively small amounts of heat enter the body with the food, by radiation from the sun or from fires. The heat arising from the food is formed by true combustion, the carbon in it is used up exactly as it is in a fire with the production of carbonic acid and water. The combustion is slower, that is all. Perhaps it may be said that combustion in the body is more thorough than in an ordinary fire, and more akin to the processes which take place when gas is burnt in a Bunsen burner. As has been stated in the section on metabolism and diet, the combustion or oxida-

TABLE LXIV.—*Showing the Metabolic Processes in a Man of 71 Kilogrammes given Food after 24 hours Fast.* (*Pettenkofer and Voit.*)

Food-Stuffs Taken.	Total in Grammes.	Water.	Carbon.	Hydrogen.	Nitrogen.	Oxygen.	Ash.
Meat Extract	12.5	3.97	2.44	0.49	1.18	2.02	2.40
Common Salt	15.1	0.27	—	—	—	—	14.83
Water	1027.2	1026.79	—	(114.56)	—	(916.47)	0.41
Oxygen	779.9	—	—	—	—	779.90	—
TOTAL	1834.7	1031.03	2.44	115.05	1.18	1698.39	17.64
Elements Excreted—							
In the Urine	1197.5	1147.44	8.25	221.59	12.51	1298.47	19.70
In the Breath	1567.2	828.90	201.30	—	—	1002.88	—
TOTAL	2764.7	1976.34	209.55	221.59	12.51	2301.35	19.70
Loss in Body	−930.0	−945.31	−207.11	−106.54	−11.33	−602.96	−2.06

Equal to a loss of 262.6 grm. of Fat, and 638.5566 grm. of Water, and 24.278 grm. Urea (or 75.5 grm. Proteid)

			N.	C.	H.	O.
C. 202.2544	=H. 70.95=N. 11.33	or 22.4 grm. Urea.	10.4	4.4	1.47	5.9
H. 31.512	C. 4.8536	and .36 ,, Uric Acid	.12	.13	.008	.102
O. 28.88	O. 6.4741	.87 ,, Kreatinin	.32	.36	.053	.12
	O. 567.606 H. 1.6185	.59 ,, Ammonia	.49	—	.100	—
		TOTAL ..	11.33	4.89	1.631	6.122

Leaving 2.4488 grammes of Hydrogen unaccounted for.

tion of the carbon and hydrogen in carbo-hydrates and fats is complete in the body. The nitrogenous derivatives of the proteids, however, can be made use of in the production of heat by further oxidation, and any calculation of the heat-producing power of food substances must include the amount yielded by them.

Before treating of the power of heat-production of food substances it will be necessary to explain the standard scale which is used to denote it. The unit of heat, termed the *calorie*,[1] is the amount of heat required to raise 1 gramme or cubic centimetre of water 1° Centigrade. Thus 20 calories represent the amount of heat necessary for increasing the heat of 20 c. cm. of water by 1°, of 10 c. cm. of water 2°, or of 2 c. cm. of water 10°, etc. The amount of water in grammes or cubic centimetres when multiplied by the increase of heat in degrees gives the corresponding number of heat-units or calories used in raising its temperature. Further terms are employed by physiologists, one to express temperature changes in large bodies, a second in recording minute variations. The amount of heat requisite to raise 1000 grammes of water 1° is called a *kilo-calorie*, and that requisite to raise 1 milligramme of water 1° a *milli-calorie*. If the temperature of 1 kilogramme of water be the same as that of another portion only measuring half a kilogramme, the number of heat-units present in the first portion is double the number in the second. An animal of 50 kilogrammes possesses twice as much heat as one of 25 kilogrammes whose body temperature is the same.

Heat-production. — Experiments on men enclosed in a chamber, or calorimeter, designed for the direct estimation of the heat given off, show that during sleep 40 kilocalories are produced; while at rest during the daytime 100 kilocalories are formed, rising to 150 kilocalories with moderate, and to 250 or 300 with active exercise. The average heat-production in the twenty-four hours by a man of ordinary weight is about 105 kilocalories per hour, or 2500 kilocalories altogether. Of this, 80 per cent. is lost by the skin, made up of 15 per cent. due to evaporation of water, 30 per cent. due to radiation, and 35 per cent. to conduction and convection; 17.5 per cent. is lost by the lungs, 15 per cent. in evaporation of water,

[1] Calorie is used throughout in this sense; great calories or kilocalories where advisable for brevity. Thousands and millions are marked off with commas, fractions with dots.

and 2.5 per cent. in heating the expired air; 2.5 per cent. is lost with the excreta. Nebelthau found that in the rabbit 16 per cent. of the total loss of heat arose from the evaporation of water.

TABLE LXV.—*Calories in the Food of an Adult per diem. Estimated by Actual Combustion.*

Playfair - - -	3,133,000	calories.
Moleschott - - -	3,159,000	,,
Wolff - - - -	3,031,000	,,
Voit - - - -	3,055,000	,,
Mean -	3,094,000	calories.

TABLE LXVI.—*Calories of Food absorbed, those for the parts passed in the fæces, and in a not fully oxidised form in the urine, subtracted.*

Rubner - 3,094,000 – (8.11 per cent.) 251,000 = 2,843,000.

If we consider, in relation to the body-weight, the equivalent heat-calories contained in the standard physiological diet for a man of 70 kilogrammes, which has been already stated to consist of 140 grammes proteid, 100 grammes fat, and 350 grammes carbo-hydrates, we find that it affords 2,878,500 calories, or 41,121 calories per kilogramme. This figure is arrived at as follows. By direct experiment Stohmann found that 1 gramme of dry egg albumin when burned in a calorimeter yields 5,735 calories of heat, a gramme of grape-sugar 3,742, and a gramme of animal fat 9,500 calories. But from the total heat obtainable from a gramme of proteid the equivalent value of the constituents of the urea derived from it and excreted in a form which does not represent full combustion must be subtracted, along with the small quantity which is passed through the alimentary tract and voided in the fæces (Rubner).

TABLE LXVII.—*Heat Equivalent of Food Elements.*

One gramme of albumin - - - -	5,735	calories.
One gramme of albumin minus urea and the portion passed in the fæces - - -	4,420	,,
One gramme of fat - - - - - -	9,500	,,
One gramme of glucose - - - - -	3,742	,,
If reckoned as starch - - - -	4,182	,,
,, ,, cane-sugar - - -	3,955	,,

TABLE LXVIII.—*The Heat Equivalent of the Specimen Diet.*

140 grammes of	proteid - -	× 4,420 =	618,800 calories.
100 ,,	fat - -	× 9,500 =	950,000 ,,
350 ,,	carbo-hydrate (as glucose)	× 3,742 =	1,309,700 ,,
590 ,,	total diet - - -		2,878,500 ,,

Body-weight, 70 kilogrammes; calories, *per kilogramme*, 41,121.

If the heat-equivalent of the 350 grammes of carbo-hydrate bodies be reckoned as starch the total calories yielded amount to 3,031,800, or 43,311 per kilogramme. A sufficient diet for a man doing a fair day's work should therefore yield about 40 kilocalories of heat for each kilogramme of his body-weight. To separate the proportion of the energy afforded by this diet into the heat-equivalent of mechanical work performed and the actual amount of heat generated, the heat-equivalent of the mechanical work must be estimated and deducted. As a general rule it may be said that one-fifth of the total energy evolved is expended on mechanical work, and four-fifths appears as heat. Deducting one-fifth from the total heat-equivalent, 2,878,500, we obtain 2,302,800 calories as the sum of the heat produced, and 575,700 calories as the heat-equivalent of the work done. Or if a day's work be considered as equivalent to 150,000 kilogramme-metres—*i.e.*, the raising of 150,000 kilogrammes one metre—and each kilocalorie as equivalent to 424 kilogramme-metres of work (Joule), the day's work can be represented in terms of heat as 150,000 $\frac{1000}{424}$, or 353,000 calories. Deducting this from the total heat-equivalent, we get 2,525,500 calories as the amount of actual heat-production.

Both these results correspond fairly well with the calculated heat-loss of the body. Vierordt gives the following figures for the daily loss of heat in man :—

TABLE LXIX.—*Loss of Heat.*

Calories.			
1,822,500 -	Evaporation of water	From skin -	87.5 per cent.
364,000 -	Radiation		
182,000 -	Evaporation of water	From lungs -	10.7 ,, ,,
84,500 -	Warming expired air		
47,500 -	Warming urine and fæces - - -		1.8 ,, ,,
2,500,500 -	Total heat-loss of the body.		

Probably one-sixth of the total energy available is the pro-

portion to be assigned to the production of mechanical work rather than one-fifth.

The production and loss of heat in the body varies in close relationship to the state of the body. If the day be divided into three periods of eight hours, one for work, one for rest, and one for sleep, we find that during the working hours as many as 216,960 calories of heat may be produced in each, 140,000 during each of the resting hours, and only 40,000 during each hour of sleep. The total of these figures amounts to 3,175,680 calories, a sum rather above that afforded by the specimen diet, but the proportion between the figures for the three periods applies equally to both. Thus we find that only about 10 per cent. of the total heat-production occurs during the eight hours of sleep, about 35 per cent. in the eight hours of rest, and 55 per cent. during the eight hours of work.

Careful observations by Ott, by D'Arsonval, and by Rubner tend to show that most adults in health produce from 2,000,000 to 3,000,000 calories in twenty-four hours when resting or only engaging in light work; when performing a hard day's labour the heat-equivalent rises to a figure between 3,000,000 and 4,000,000.

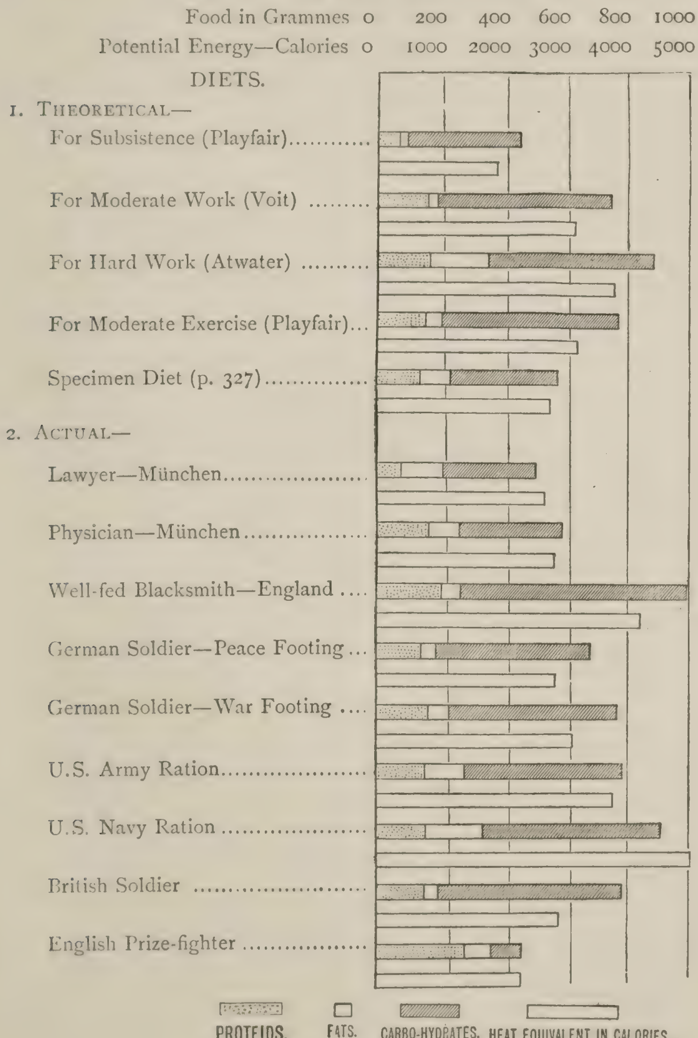
In Diagram VII. the heat-equivalent of the diets taken by various classes of men, as calculated by different observers, is graphically shown.

Rubner has calculated that, given a standard weight of 67 kilogrammes, a fasting man produces *per diem* 2,303,000 calories, brainworkers only a little more, 2,445,000 calories, while soldiers in times of peace and day-labourers (probably non-energetic types) produce 2,868,000 calories. Skilled labourers manufacture 3,362,000, and miners 4,790,000 calories. A further class attains a heat-production of 5,360,000 calories, and is represented by lumberers and out-of-door labourers, especially when they have to face intense cold during the execution of their work.

It may be stated as a general rule that the food, to be sufficient for the proper production of the energy, whether it be transformed into mechanical work or into heat, should under ordinary circumstances be equal to from 35 to 40 kilo-calories per kilogramme of body-weight.

The Seat of Heat-production.—A few words may be added with regard to the tissues in which the oxidation of the calorific elements, derived from the food and conveyed to them by the blood, chiefly takes place. When a muscle contracts, a certain amount of chemical change, chiefly consisting in oxidation, precedes the active movement. The heat-equivalent, however, of this chemical reaction is much greater than the heat-equivalent of the work done. At least four-fifths of the energy or heat produced takes no part in the mechanical action; only one-fifth or one-sixth suffices, the remainder appears as actual heat. The amount of heat given off by the chemical changes which are necessary to initiate the total

DIAGRAM VII.—Showing the Heat Equivalent of various Dietaries (drawn partly after Stewart).



muscular work of the body during an ordinary day's labour forms the greater part of the heat produced in that period. For instance, the work of the heart muscle has been estimated as equal to 30,000 kilogramme-metres in the twenty-four hours. If the energy produced by chemical changes to effect such an amount of work is equivalent to five times the visible result, the total energy expended will be equivalent to 150,000 kilogramme-metres, or 353,000 calories of heat; and, as most of the mechanical work of the heart is used in overcoming the friction of the blood-vessels, a great part of its energy is in the end transformed into actual heat. The energy evolved by the heart of an adult during the twenty-four hours is equal to that necessary to raise a man of eleven stone about 7000 feet, or about twice the height of Snowdon. If we add to this the 13,000 kilogramme-metres of work done by the respiratory muscles, or rather the equivalent energy production of 65,000 kilogramme-metres, equal to 153,000 calories, during the day, the total of 215,000 kilogramme-metres is obtained, or 506,000 calories of heat produced by the circulatory and respiratory mechanisms alone, about one-fifth of the total heat-production during ordinary labour. But we have seen that about 320,000 calories are produced during the eight hours allowed for sleep. If we divide the total heat given off by the heart and the respiratory muscles during the twenty-four hours by 3, we get 168,000 calories as the result. The circulatory and respiratory movements are, however, slower and less possible during sleep, and 150,000 calories may be taken as their heat-equivalent. If the movements of the involuntary muscular tissue of the intestinal canal be also taken into account, it is easily seen that during sleep a large proportion of the heat produced in the body is derived from the chemical changes antecedent to and necessary for muscular contraction.

Hein found that a man gave off 283,000 calories of heat when performing 27,700 kilogramme-metres of work per hour. But as 27,700 kilogramme-metres of work are represented by about 65,300 calories of heat, the amount of the heat-equivalent produced, even if the striped muscles only produce four times as much heat as work, is almost equal to the total evolved. Again, even when at rest muscles produce some heat. The muscles of a dog's leg have been found to remove 150 c.c. of oxygen per kilogramme per hour from

defibrinated blood. It has been calculated that one-tenth of the total heat-production of the body at rest may be afforded by quiescent muscular metabolism.

The glands of the body also produce heat, but to a much less extent than the muscles. Many of the chemical changes occurring in the glandular organs are heat-producing, but some of the reactions which take place in them are synthetic in nature and tend to absorb rather than evolve heat. The central nervous system ranks as a heat-producing centre, but its metabolism is very feeble when compared with that of the muscles. The main source of the energy which appears as heat and as muscular work is undoubtedly the oxidation of food substances; but it is as yet unknown how part of the energy is converted into mechanical work, and part into heat. It has been suggested that the energy derived from chemical reactions is first converted into electrical energy, which is in large part squandered in the production of heat.

Pembrey and Hale White (*Journ. of Phys.*, xix., p. 477) conclude from a consideration of experiments on hibernating animals that their body temperature is maintained by the heat produced from the muscular contractions of the heart, the friction resulting from the passage of the blood through the vessels, and the movements necessary for respiration. During their winter sleep any increase in body temperature is accompanied by the disengagement of carbonic acid gas, and at the time when activity again begins, this development of the gas is so great as to resemble a sort of explosive action.

CHAPTER XVI.

STIMULANTS.

ALCOHOLS :—Nature—Universal Use—Actions on the Body—Influence on Digestive Processes—On Saliva—Peptic and Pancreatic Digestion—Action of Fusel Oils.
NON-ALCOHOLIC :—Tea—Coffee—Cocoa—Coca.

Alcohols.—The monatomic alcohols are neutral hydrates in which an atom of hydrogen in certain hydrocarbons has been replaced by the radical hydroxyl (OH). In the methyl compounds the radical CH^3 becomes CH^3-OH, or methyl alcohol, one atom of hydrogen in the hydride (Methane, CH^3H) being replaced by hydroxyl. Similarly, ethylic alcohol is ethyl hydrate or C^2H^5-OH, propyl alcohol C^3H^7-OH, butyl alcohol C^4H^9-OH, and amyl alcohol C^5H^{11}-OH. The higher alcohols in the series above butyl alcohol have several isomeric modifications. Ethyl alcohol, $C^2H^6O = CH^3\text{-}CH^2\text{-}OH$, is the ordinary alcohol of wines and spirits, and when absolutely pure is a colourless, mobile liquid, with a density of 0.8095 at 0°. It boils at 78.3° Cent., mixes with water in all proportions, causing the evolution of heat and contraction of volume, and, because of its lower boiling point, when heated distils over more quickly than water, and can thus be separated from it. Methyl alcohol, or wood-spirit, when pure is also colourless, but has a nauseous taste and odour. It boils at 66.5°, and has a density of 0.8142 at 0° Cent. Amyl alcohol of fermentation (that produced by chemical decomposition is different in its properties, although isomeric) is a colourless liquid, having rather an unpleasant odour. It boils at 132°. Its density at 0° is 0.8184. It is better known by the name of fusel oil. Spirit produced by the fermentation of grain or potatoes, instead of from malt, contains much of it.

It is doubtful if there has ever been in this world a race of men ignorant of the stimulating and exhilarating effects of the products of the fermentation of starch and sugar. At least all races, from the earliest times to which we can go back, possessed some form of fermented liquor. The Teutonic races drank mead, made from a mixture of honey and water, and fermented. The Japanese make use of Saká, a sort of beer made from rice. The South Sea Islanders, cut off for ages from intercourse with their fellow-men, contrived to extract a similar beverage from the juice of the cocoa-nut. Nearly all those early products contained only a small percentage of alcohol, and were drunk in large bulk. It is almost unnecessary to observe that all civilised nations are adepts in preparing seductive fluids, which contain alcohol as a *conditio sine qua non*. One of the questions which have been discussed for ages, and which will probably long remain a subject of contention, "Is alcohol a food or a poison?" has been satisfactorily answered by physiologists during the last few years. But calm and dry statements of fact by scientists rarely carry conviction to the public, who are too often misled by deluded fanatics and their theatrical and biassed harangues. As in most issues the truth lies between the two extremes: alcohol is a food under many and varied circumstances, a poison under others, and it serves as a valuable stimulant in many cases where its use, without the least doubt, materially contributes to save life. A poison if taken in too large amount at one time or in smaller quantities too frequently; a food when the diet taken contains too small a proportion of the elements required to equalise the waste of bodily metabolism; it is invaluable as a restorative on such occasions as the crisis of a fever, or the shock which follows an accident or an operation.

The effects ascribed to alcohol by mankind are protean. It is drunk in the tropics to cool the body, in the cold of a northern winter for the sake of warmth; it is taken to drive away muscular fatigue or to rouse the flagging brain, to steady the trembling hand, or to drown the memory of misfortune. Many of these effects appear to be contradictory and impossible, but they are all in a sense founded on physiological actions. It is a somewhat difficult task to sketch in a few words the various effects of alcohol on the different organs and functions of the body. For the sake of clearness we may first

note its actions on the general bodily metabolism and the nervous system, and then glance at its more local effect upon the processes of digestion.

Alcohol is rapidly absorbed by the mucous membrane of the stomach, but even before absorption, if in a concentrated form, reflex stimulation of the heart and circulation occurs. The heart beats more rapidly and with greater force, the blood-pressure rises, even although the blood-vessels, especially those of the skin, dilate, causing a feeling of increased warmth. After the entrance of alcohol into the blood-stream—it is absorbed more readily by the blood-vessels than by the lacteals—a change may be observed in the corpuscles, the amœboid (intrinsic) movement of the white blood-corpuscles being first increased but soon after markedly diminished, while the red corpuscles part with the oxygen contained in their oxy-hæmoglobin much less readily. As this power of readily yielding oxygen governs the metabolism of the body and the consequent production of its heat, alcohol serves as a tissue-sparer; but, again, it accelerates the rapidity of the circulation and thus counteracts to some extent the diminution in its oxidising power. Small quantities taken at moderate intervals do not interfere with oxidation; in larger doses, and if taken frequently, imperfect combustion of fats is manifested by the deposition of fat in the tissues, and by the occurrence of fatty degeneration of the organs.

In health we may fairly state that, taken infrequently and in small quantities (2 oz. in the day the *maximum*), it can do no harm, and probably does some good in stimulating the appetite, as we shall see later. If indulged in too freely it acts deleteriously.

In disease, however, especially in cases of pyrexia, its power of diminishing oxidation renders it a most valuable adjuvant to other treatment. It also acts in such cases as a food, owing to its oxidation in the tissues. For long the question of the oxidation of alcohol in the body remained doubtful. Lallemand, Perrin, and Duroy asserted that it was all excreted unchanged by the emunctories. Anstie, on the other hand, proved that only a slight proportion was passed out by the kidneys, and then only if much had been taken. Hammond at length placed the matter on a secure basis by showing that the addition of alcohol to a diet insufficient to maintain the body-weight, not only prevented the loss, but converted it into a gain.

We may state three propositions as to its action as a food—

1. With a *diet greater than necessary* to keep the body-weight steady, alcohol does harm, is superfluous, and DECREASES THE RATE OF INCREASE IN WEIGHT.

2. With a *diet sufficient to maintain* the body-weight, the addition of alcohol to it may cause SOME LOSS OF WEIGHT.

3. With a *diet insufficient to keep the weight steady*, alcohol is of service, the WEIGHT REMAINING THE SAME OR EVEN INCREASING.

Little of the alcohol taken by the mouth appears in the urine unless the amount drunk be excessive. The tests which were relied on up to a recent date for the detection of alcohol in the urine are very untrustworthy. The most rigid teetotaller with their aid can be shown to excrete large quantities of alcohol. The small amount excreted by the kidneys compared with that taken in arises partly from exhalation with the expired air, partly from oxidation of the alcohol in the body. After absorption the chief action of small quantities of alcohol is exercised upon the circulation. The nerves which carry the fibres set apart for conveying accelerating impulses from the brain to the heart are stimulated, the heart beats more rapidly and powerfully, the blood-pressure in the arteries rises in spite of their increased calibre, owing to the stimulation of the vasomotor nerve fibres which influence the size of the vessels, and all parts of the body, for the time, are better nourished. Thoughts become clearer, the brain more acute; the misanthrope brightens, the timid becomes bold, the bold still more venturesome, even "pot-valiant." But in some individuals alcohol has an opposite effect: they become, even after small quantities, sleepy, heavy, stupid, and often cross. The first and larger class experience the exhilarating effects which follow an increased flow of blood through the vessels of the brain, the second the depressing results of a diminished supply of blood to the brain owing to the large quantity required to fill the dilated vessels of the skin. Such results, if brought about at intervals, do no harm, but if frequently repeated the necessary amount of alcohol for their production has gradually and progressively to be increased, while, although the effects are pleasant and stimulating at the time, the heart is left more exhausted after they have passed off than before, and all the organs of the body experience the inevitable rebound which follows abnormal stimulation. Probably the occasional indulgence

in a sufficient amount of alcohol to cause the earlier symptoms produced by its use may be beneficial rather than harmful, if not repeated too often, from the general stimulation and temporary "rousing up" of the organs and tissues. But alcohol should never be taken by those exposed to great cold, as by increasing the transpiration of heat from the dilated vessels of the skin much of their body-heat is lost, and they are less able to withstand the cold afterwards from exhaustion of their powers of producing body-heat. The same mode of reasoning applies to those doing continuous and heavy work, and to those living in very hot climates; alcohol at first stimulates them, but also cools them by increasing perspiration, then renders them less capable of withstanding the toil or the heat from the consequent exhaustion.

TABLE LXX.—*Showing the Proportion of Alcohol and other Constituents in Spirits and Wines.*

Liquor.	Alcohol %	Solids %	Ash %	Sugar.	Acidity.
Absolute Alcohol	99.5–100	—	—	—	—
Proof Spirit	49	—	—	—	—
Whisky (Parkes)	50–55	0.6	Trace.	0	0.04%
(Chittenden)	50–51	0.3284	0.004	0	Acid
Brandy (P)	45–55	1.2	0.05–0.2	0	0.2%
(C)	47–48	0.43	0.0054	0	Acid
Gin (P)	49–57	1.2	0.1	0	0.04%
(C)	51	0.29	0.009	0	Acid
Rum (P)	50–60	1.0	0.1	1	0.1%
(C)	50–51	0.3	0.007	—	Acid

RED WINES (K)—	Alcohol.	Tannin and Colouring Matter.	Sugar.	Free Acid.
Rhine Wine	10.08	0.16	—	0.52
Hungarian	9.65	0.13	—	0.59
Burgundy	11.15	—	—	0.53
Bordeaux	9.07	0.22	—	0.59
(Chittenden	9.7–10.0	Total Solids 3.3%, Ash 0.6%, Strongly acid.)		
WHITE WINES (K)—				
Rhine	11.45	—	0.37	0.46
Moselle	12.06	—	0.20	0.61
Riesling	12.90	—	0.01	0.65
SWEET HUNGARIAN (K)—				
Tokayer	12.74	18.34	14.99	0.52
Ruster	11.08	23.64	21.74	0.51

FORTIFIED WINES (K)—				
Port '65	21.91	8.83	6.42	0.45
Sherry '70	22.9	3.78	1.88	0.44
Madeira '70	19.11	5.22	3.46	0.48
Marsala	20.44	4.94	3.48	0.39
Malaga '72	16.14	21.23	16.47	0.42
SPARKLING WINES (K)—				
Champagne	11.75	13.96	11.53	0.58
Rhine	12.14	12.14	8.49	0.57

BEERS—	Alcohol.	Malt.	Ash.	Sugars.	Albuminoids.
Münchener Löwenbrau (L)	4.45	7.09	0.36	6.15	0.57
English Bitter (L)	6.78	5.42	0.24	4.22	0.16
English Mild (L)	8.45	6.74	0.43	5.77	0.26
Berliner Weiss (W)	1.9	5.7	—	—	—
Bass (C)	4.0	4.425	0.35	—	0.73
Stout (C)	5.5	5.4	0.36	—	0.73

(P) = Parkes. (Acidity by Parkes in terms of tartaric acid per cent.)
(C) = Chittenden.
(K) = König. (Free acidity per cent., probably as oxalic acid.)
(L) = *Lancet* Office (1895).
(W) = Willoughby.

Influence of Alcohol on the Processes of Digestion.—It is apparent from a glance at Table LXX. that there are very pronounced differences between the various wines and spirits, both in the proportion of alcohol which they contain and in their other constituents. From the experiments of Sir William Roberts, and of Chittenden and Mendel, on the action of these different drinks on the chemistry of digestion, it may be assumed with confidence that spirits influence it only in respect to the proportion of alcohol they contain, and that, with wines and malt liquors, the effects produced depend upon the solid matter and extractives contained by them, or upon their acidity.

Spirits when taken "neat" act on the mucous membrane of the mouth, if kept in it any length of time, by precipitating the albumin of the cells and blood serum. If swallowed quickly, this action is inhibited by the increased flow of saliva induced. When it reaches the stomach in a concentrated form and in large quantity, the reflex results, already mentioned, may be so greatly intensified as to rapidly cause insensibility or even death. If sufficiently diluted by the saliva or by the contents of the stomach, little effect on the mucous membrane of that organ is produced; if more concentrated, and taken on an empty stomach, irritation of the mucous membrane ensues, and if the irritation be repeated frequently, passes into a state of catarrh. (Chart XVII.)

As has been said, alcohol stimulates the flow of saliva, but when we look into its action on the special properties of that secretion some important facts are obtainable. The following table from Roberts will suffice to illustrate this point in a brief but striking manner:—

TABLE LXXI.—*The Effects of Alcoholic Liquors on Salivary Digestion. Normal time taken, 4 minutes.*

	Time taken before the Achromic Point was reached.				
Amount of Alcoholic Liquor* per cent. in the Digesting Mixture.	Proof Spirit.	Whisky.	Brandy.	Sherry.	Hock.
0.25	—	—	—	8 min.	16 min.
0.5	—	—	—	30 ,,	80 ,,
1.0	—	—	—	No action beyond soluble starch.	
2.0	—	—	—	No action.	
5.0	4.0 min.	4 min.	4 min.	—	—
10.0	4.0 ,,	30 ,,	Very slow.	—	—
20.0	4.0 ,,	Very slow.	Nil.	—	—
40.0	8.0 ,,	Nil.	,,	4 minutes (after neutralisation).	
60.0	14.0 ,,	,,	,,	—	—
70.0	20.0 ,,	,,	,,	—	—
90.0	Very slow.	,,	,,	—	—

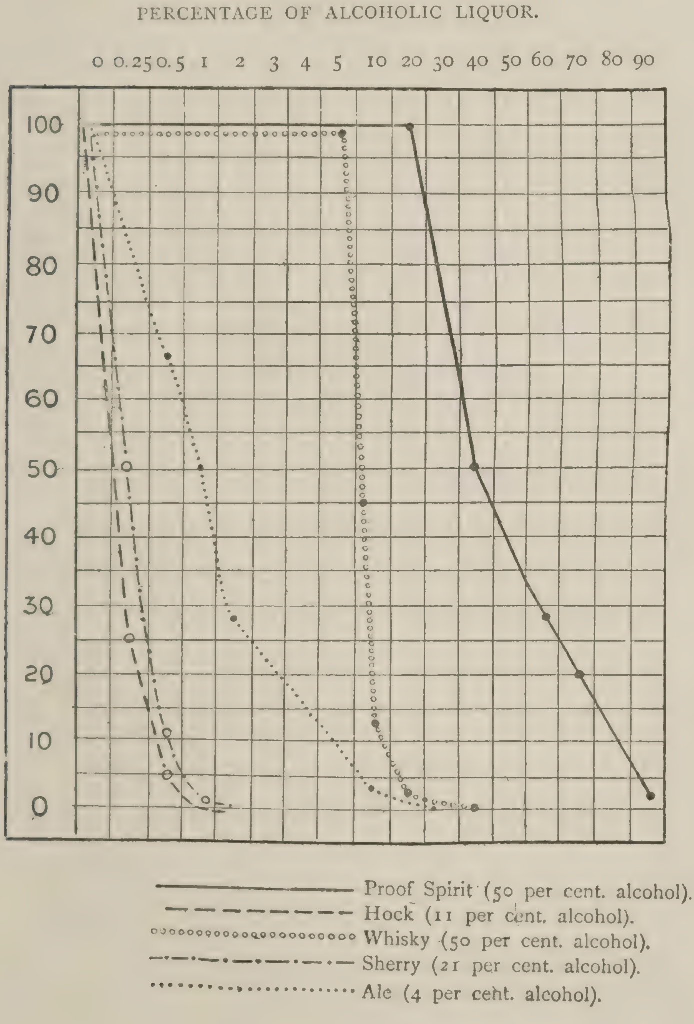
* These figures represent the percentage of alcoholic liquor in the mixture during digestion, not the proportion of pure alcohol.

Alcohol in the form of proof spirit has no retarding influence even when present in a strength of 20 per cent., or 10 per cent. of absolute alcohol; when present as 40 per cent. the amylolytic power is only half as great, although 90 per cent., or 45 per cent. of alcohol, does not entirely abolish all action. Whisky and brandy with practically the same alcoholic strength do not affect the action of ptyalin when present in the proportion of 5 per cent. Whisky present as 10 per cent. causes a greater retardation than 70 per cent., and brandy in the same proportion acts as strongly as 90 per cent., of proof spirit.

Still more striking are the results obtained when sherry and hock are added. These wines, and especially hock, delay the conversion of starch by ptyalin most markedly, but this cannot be due to the amount of alcohol contained in them, and evidently depends on the acids present. Neutralisation of a solution containing 40 per cent. of each of these wines causes a return to the normal period of conversion.

As sherry contains about 22 per cent. and hock only 11 per cent. of alcohol, 0.25 per cent. of sherry only represents about

CHART XVII.—Showing the Relative Actions of Alcohol, Whisky, Sherry, Hock, and Ale on Salivary Digestion.



0.055 per cent. of alcohol, and of hock about 0.027 per cent. Forty per cent. represents 8.8 per cent. of alcohol in the case of sherry, and 4.4 per cent. in the case of hock, percentages of pure alcohol which do not affect the rapidity of salivary digestion in themselves. The curves given in Chart XIX. (p. 353) make it clear that the increase in the action of whisky and brandy in retarding salivary amylolysis over the action of corresponding solutions of pure alcohol is not due to the presence of the higher alcohols or "fusel-oils." In fact, amylic alcohol is the only one in which a 1 per cent. solution does not tend to increase rather than decrease the action of ptyalin; methylic alcohol up to 5 per cent. aids amylolysis. Whisky and brandy up to 5 per cent. do not retard the salivary digestion of starch, and in higher proportions up to 10 per cent. exert no deleterious action if their acidity be neutralised. Rum acts more adversely, 5 per cent. reducing the relative digestive power to 50, but 10 per cent. has no such retarding action after neutralisation.

TABLE LXXII.—*The Action of Brandy and Rum on Salivary Digestion.*

Brandy. Proportions Present.	Appearance of Achromic Point (Saliva 1 : 5).	Rum. Proportions Present.	Appearance of Achromic Point (Saliva 1 : 10).
0 %	2 minutes	0 %	3 minutes.
5 ,,	12 ,,	5 ,,	16 hours.
5 ,, (Neutralised)	2 ,,	10 ,,	No conversion.
10 ,, Do.	2 ,,	10 ,, (Neutralised)	3 minutes.
(5 ,, Absolute alcohol)	2 ,,	(5 ,, Absolute alcohol)	3 ,,

The marked retarding action of rum is therefore not due to the alcohol in it but to the large amount of volatile acid bodies.

An interesting analysis showing the effect of age on wines is the following by Berthelot (*Comptes Rendus*, 1879):—

TABLE LXXIII.—*Analyses of New and Old Wines.*

	Port Wine. 100 Years Old.		Port Wine. 45 Years Old.
Specific gravity (at 10°)	0.988	......	0 991
Total residue at 100° %	3.360	......	5 300
Sugars, reducing, %	1.250	......	3.150
Sugars, after dilute acid, %	1.290	......	3.680
Acid (as tartaric; gms. per litre), %	5.170	......	5.460
Tartaric ether, %	1.110	......	1.170
Cream of tartar, %	0.270	......	0.420
Alcohol, %	15.900	......	16.100
Examination of the deposits showed—			
Sugar, reducing, %	1.250	......	3.150
Cane-sugar, %	0.040	......	0.530

The total residue of old wine is less than that of new, and contains scarcely any cane-sugar, probably due to the slow inverting action of the organic acids in it. The tannin also decreases, while the glycerine increases. All these facts explain why an old, fully matured wine is less apt to cause digestive disturbances than a new and raw sample.

Table LXXIV.—*The Constituents of Wine.* (*Wynter Blyth.*)

Water. Grape-sugar (0 to several per cent.).
Alcohols, mainly ethylic, but also small quantities of the higher alcohols, as propylic, butylic, amylic, and others.
Albuminoid residues. Aldehydes (mainly ethylic).
Isobutylglycol. Acetal. Furfurol. Acetic acid.
Succinic acid. Tartaric acid. Calcium tartrate. Gum.
Malic acid (in bad seasons). Colouring matters. Glycerine.
Organic acids in combination. Extractive matters.
Esters—acetic, caproic, caprylic, butyric, and tartaric. Tannin.
Mineral matters. A few ferment cells.

The action of alcoholic liquors on peptic digestion has been studied exhaustively by Sir William Roberts, and, more recently, by Professor Chittenden and L. B. Mendel in America. Their results do not apply in all respects to true gastric digestion, as, owing to the experiments having been exclusively performed *in vitro*, no evidence could be obtained of the influence of alcohol on the actual gastric secretion or on the movements of the stomach walls. The action of alcohol and alcoholic liquors on the proteolytic power of pepsin and hydrochloric acid outside the body must, however, have much to do with their power in the body, and results obtained from such observations have a decided value. These observers found that the action of alcohol in all alcoholic liquors depended largely on its percentage, entirely so in the class of spirits, and to a less extent in wines and malt liquors. One or two per cent. of absolute alcohol—that is, about 2 to 4 per cent. of proof spirit—tends slightly to increase the peptonising power of the gastric juice. Up to 15 per cent. of absolute alcohol no perceptible retardation occurs; with 15 to 18 per cent. digestion may be reduced one-quarter or even one-third, although the retardation varies greatly with the strength and activity of the gastric juice, and the digestibility of the proteid. The greater the power of the gastric juice is, the less the retardation. A percentage of 20 or more strongly inhibits the digestive process. The common

spirits, whisky, brandy, rum, and gin, act proportionally to the quantity of alcohol contained in them. In the presence of 3 per cent. of whisky digestion appears to be slightly increased, 20 per cent. reduces it one-fourth. The common idea, which indeed is almost universally held, that the higher alcohols, as amylic, methylic, and propylic, the so-called fusel-oils, act deleteriously on the gastric processes, is not confirmed by actual experiment. Indeed, small quantities increase the proteolytic power of the juice. Wines and malt liquors with less than 10 per cent. of alcohol delay gastric digestion rather because of the various solid matters contained in them than from the amount of alcohol. This is especially the case in malt liquors when used in large quantities, and arises from the large proportion of extractives present. Small quantities of wine may somewhat increase digestion, similar amounts of beer or ale seem to have no influence on it. (Chart XVIII.)

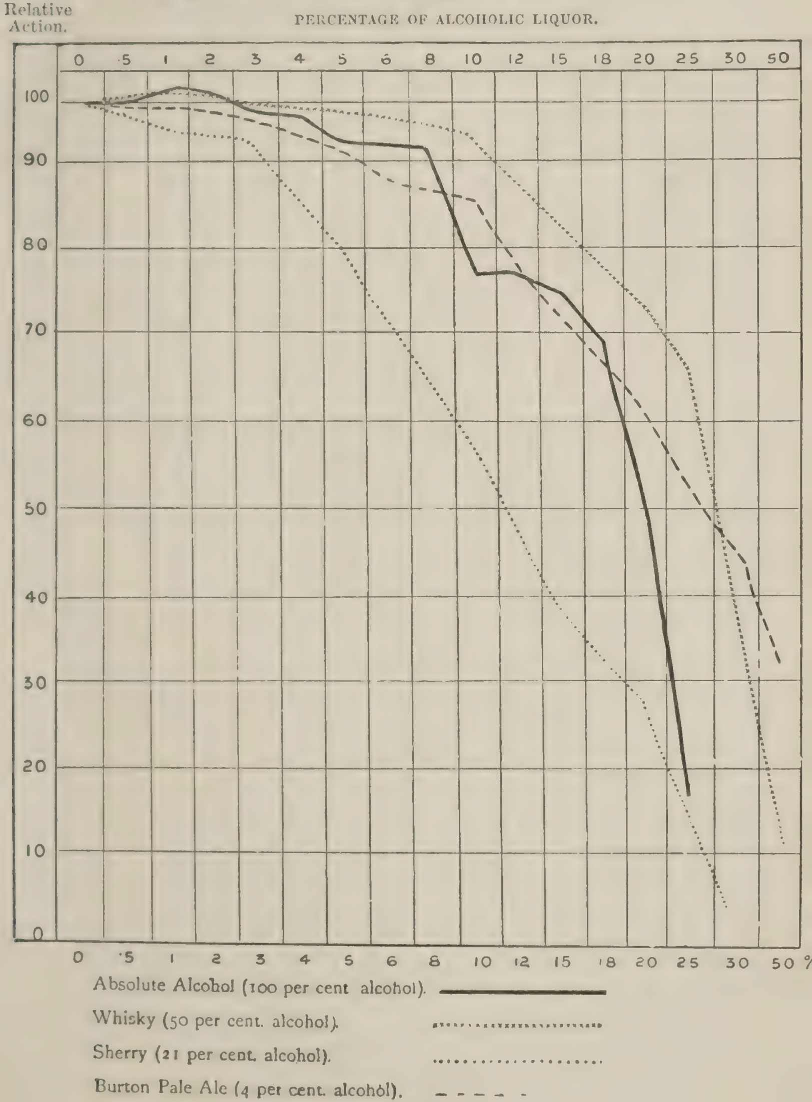
Pure spirits can therefore be taken in small quantities and well diluted, without harming peptic proteolysis, and possess the advantage over wines and malted liquors of not hindering that process while containing a somewhat larger proportion of alcohol.

It must be kept in mind in judging of the probable effect of spirits on gastric digestion in the body that the water generally added to them brings the percentage of alcohol in the solution below that of many wines, and even beers, which are taken undiluted. Thus an ounce of whisky with 50 per cent. of alcohol, with 14 ounces of water, makes a drink containing only .5 of an ounce of alcohol in 15 ounces, or 3.3 per cent. This is exactly the proportion which appears to aid gastric digestion, and even it is lessened by the addition of the secretion of the salivary and gastric glands. Sherry and port when undiluted act much more deleteriously, owing to their percentage of alcohol (21-23), and to the effect of the solid matters contained in them.

The information which we possess regarding the action of alcohol on the pancreatic digestion of proteids has necessarily been obtained from artificial experiments, either by the use of an artificially prepared pancreatic juice, or by the use of pancreatic juice itself, obtained by means of a fistula. Roberts has found that the action of wines and beer on the activity of the tryptic ferment is slight, and that stronger spirits only retard its action when present in a proportion of 5 per cent. of absolute

CHART XVIII.—Showing the Relative Actions of Absolute Alcohol, Whisky, Sherry, and Ale, on Peptic Digestion.

Drawn from data by Chittenden. Normal peptic activity is taken as 100, and the increase or diminution of power in the pepsin-hydrochloric acid solution on the addition of the different liquors inserted in terms of the normal figure. The percentage figures do not refer to the amount of alcohol in the resultant mixture, but to the proportion of alcohol containing liquid added.



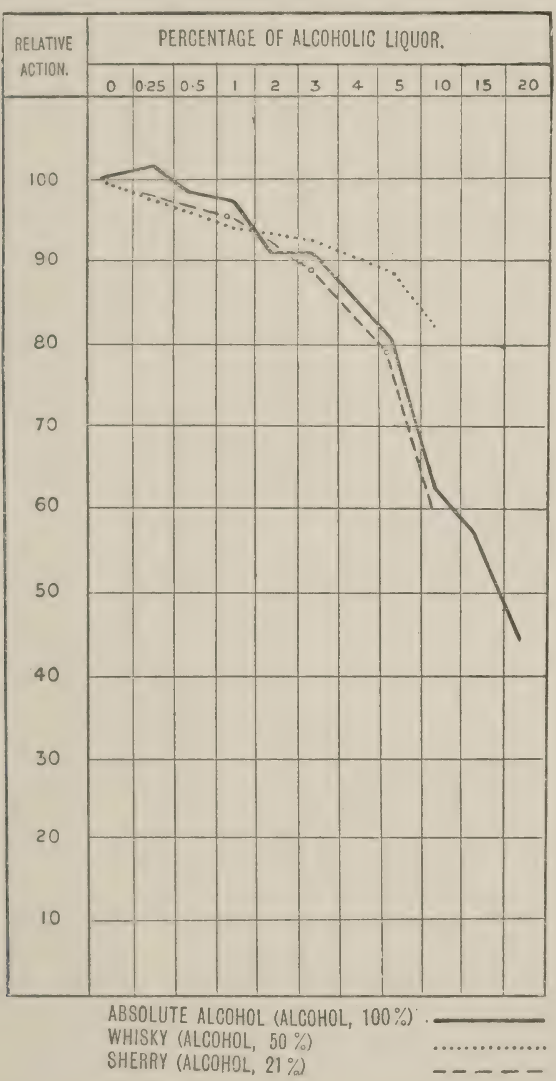
alcohol or above it. With 10 per cent. of alcohol digestion goes on to full completion, but the normal duration of the process is considerably lengthened. As alcohol is rapidly absorbed by the mucous membrane of the stomach, it is very unlikely that any such proportion can ever be present in the duodenum during life; therefore alcohol taken by the mouth can have little direct effect upon tryptic digestion in the body. Chittenden and Mendel found, in the investigation referred to above, that the retardation of digestive action by trypsin from the addition of wines in artificial experiments is due almost entirely to the acids present. The alcohol plainly exerts some retarding influence upon the proteolysis, but the delay is exactly proportional to the amount of alcohol contained in each specimen, as these observers showed by using the distillates from different classes of wines. For instance, claret, with a small percentage of alcohol, and sherry, which contains double the amount, react exactly contrary to what we should expect. The relative digestive action in the presence of 10 per cent. of sherry is 61.5, and with 10 per cent. of claret only 36.2. Sherry contains a considerably larger amount of solid material than claret, and the difference in the retarding action is ascribed by these observers to the higher acidity of claret. (Chart XIX.)

Alcohol acts upon the pancreatic ferment, amylopsin, in a similar manner to its action, already described, upon the corresponding salivary ferment. That is to say, that beer and wines retard its action owing to the acidity contained in them, while the alcoholic strength of spirits in solution requires to be above 10 per cent. of absolute alcohol before any great slowing can be observed.

Chittenden (*Journal of Physiology*, xii. 3, p. 220) found that 2.5 c.c. of absolute alcohol per kilogramme of the weight of a dog could be given for 8 to 10 days without causing any marked effect upon the dog's proteid metabolism. As alcohol does not contain nitrogen it slightly diminishes proteid exchange, but, although the results are not very definite, it must have some action on the proteids of the body, as the amount of uric acid excreted rises above the normal, even if the total outgo of nitrogen be lessened. Duogány and Tibáld (*Ungar. Arch. f. Mediz.*, iii. s. 189), experimenting on dogs, corroborate Chittenden's observation except in so far that they found the nitrogen exchange to remain equal to the normal with large

CHART XIX.—Showing the Relative Actions of Absolute Alcohol, Whisky, and Sherry on Tryptic Digestion.

The arrangement of the Chart is similar to that of No. XVIII., already fully explained.



doses of alcohol, while after small doses its outgo increased. The quantity of uric acid is increased after small doses of alcohol, but unchanged when large amounts are given. The excretion of phosphorus varies similarly to that of nitrogen, while in small or moderate amounts of alcohol the sulphur is increased, but is diminished when much alcohol is given.

Tichen, of Jena, places the maximum daily amount of absolute alcohol which can be taken without detriment to the nervous system at 30 to 40 grammes (1-1.5 oz.), represented by about a litre of beer (1.5 pint), with 3.5 per cent. of alcohol, or $\frac{3}{10}$ths to $\frac{4}{10}$ths litre of white wine ($\frac{1}{2}$ to $\frac{3}{4}$ pint), with 10 per cent. of alcohol. On each occasion when the portion drunk contains no more than 25 grammes of ethyl-alcohol diluted with ten times its weight of water, or equal to about 9 per cent. of alcohol, a stimulating effect follows, lasting for fifteen to thirty minutes, succeeded by a diminution of energy which continues for several hours. Larger amounts taken at one time shorten the first stage and prolong the second. The quantity noted above as the daily maximum, when taken at different times during the twenty-four hours, can bring about the greatest possible duration of the stimulating effects.

Allusion has already been made to Hammond's observations, in which the metabolic balance of the body shows an increment when alcohol is taken with an insufficient diet, but suffers loss when it is taken as an adjunct to sufficient or excessive food. Somewhat similar results have been obtained by Duogány and Tibáld (*Ungar. Arch. f. Mediz.*, iii. s. 189) from metabolic experiments upon dogs. They find that when dogs are kept for some days on a diet on which their weight remains constant, the addition of small doses of alcohol (9 c. cm.) to their daily food increases the output of nitrogen, phosphoric acid, and sulphur in the urine, which is at the same time increased in quantity. Uric acid is also excreted in greater amount. With larger doses (30 c. cm.) the output of these bodies, save uric acid and the quantity of urine passed, are diminished; the uric acid shows no change from the normal.

Comparing the effects of the higher alcohols or fusel oils on digestion of starch in the mouth, and of proteids in the stomach and bowel, as figured in Charts XX. and XXI., it may at once be seen that they exert rather a favourable action, except in the case of amylic alcohol, on the salivary ferment, but retard both peptic and tryptic proteolysis, the latter especially. The deleterious effects are generally in direct relationship to the weight of the alcohol, isobutylic being the heaviest and the most active, methylic alcohol the lightest and least harmful. The

amount of fibrin digested by pepsin and hydrochloric acid is actually increased when these alcohols are present in small quantities, an increase which is most marked with propylic and methylic alcohols. Trypsin in the presence of small quantities of these two alcohols is slightly increased in power, but a trace of amylic or isobutylic alcohol, or the presence of the other two above 0.25 per cent., serves to diminish its activity. From these data it is permissible to state that the presence of fusel oils in spirits does not cause derangement of digestion *per se*. As, however, the classes of spirits containing them are not so palatable as more mellowed brands, and as their partakers seldom dilute them to any extent, the evil effects of raw, neat spirits, which are usually ascribed to the higher alcohols, are more probably due to the non-dilution of the spirit.

We may briefly summarise the present state of our knowledge as to the action of alcohol and its uses as a food accessory.

1. It is to some extent a food, but is seldom taken except as a stimulant.

2. It can be used up in the body as a source of energy and heat, but the heat produced by it is rendered less than useless owing to the greater heat-loss brought about by the dilatation of the vessels of the skin.

3. Alcohol is of no use to healthy men who take sufficient food for their daily wants.

4. In moderate doses, and well diluted, it is not harmful to healthy men under ordinary conditions.

5. Alcohol acts injuriously in all cases of exposure to great cold, or of severe and continuous exertion, such as in Arctic expeditions or mountain-climbing.

6. If taken with meals in moderate doses it is often beneficial, as, after much of the alcohol has been absorbed, the secretion of hydrochloric acid increases to often more than double the proportion to which it would otherwise attain. The secretion of acid also continues longer than when no alcohol has been taken.

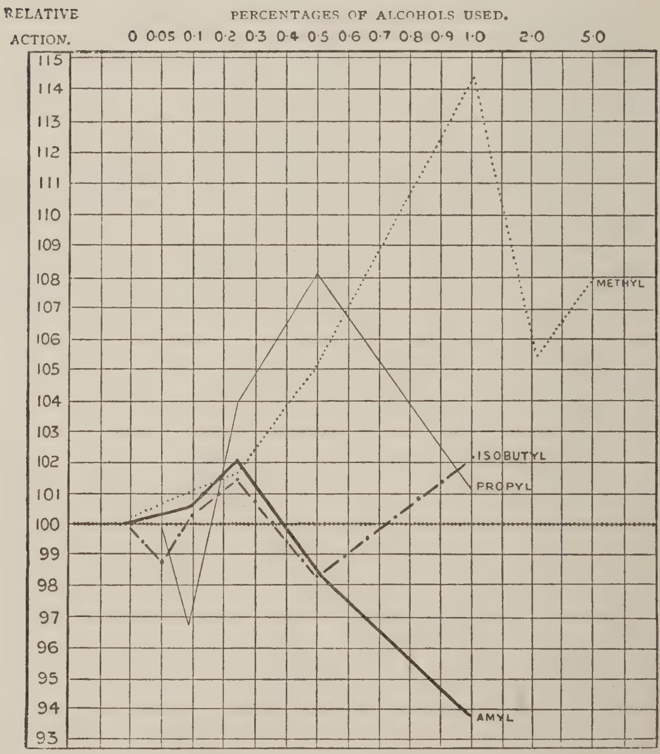
7. Alcohol seldom has this stimulating effect if the stomach be diseased.

The Action of Tea and Coffee.—The beverages obtained from the tea-leaf or the coffee-berry are not, in the proper sense of the word, foods; they act purely as stimulants, although in a different manner from alcohol. The stimulating effect is in each

case due to an alkaloid, theine in tea and caffeine in coffee, which are identical in chemical structure. The flavour and aroma are due to the presence of volatile oils. Neither the alkaloid nor the volatile oils seem to have any inhibitory effect on the

CHART XX.—Showing the Relative Actions of the "so-called" Fusel Oils on Salivary Amylolysis.

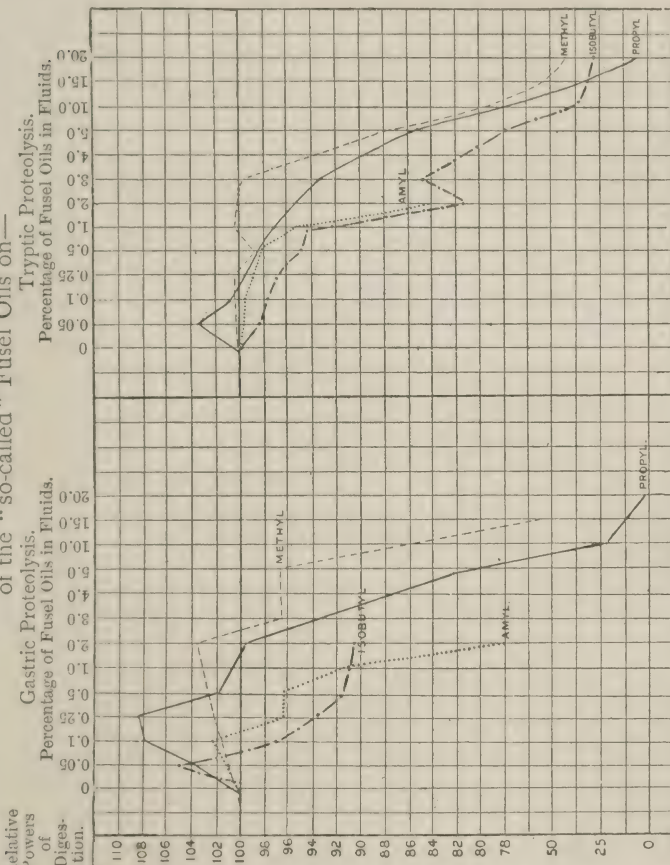
(From data by Chittenden.)



digestion of starch or on the peptic digestion of proteids. Strong infusions of tea or decoctions of coffee exert a very marked inhibitory action on all processes of digestion. This is almost solely due to the presence of tannin. As weak a solution as 1 in

5000 of tannin is sufficient to arrest the action of saliva on starch. Roberts has calculated that the amount of tannin contained in a 5 per cent. infusion of tea fully accounts for

CHART XXI.—Showing the Relative Action (data from Chittenden) of the "so-called" Fusel Oils on—



100 represents the full power of the peptic and tryptic digestion in the mixtures used before addition of the fusel oils.

its inhibitory effect on salivary digestion. For, if the tea used contains 8 per cent. of tannin and three-quarters of this are dissolved in the infusion, the resulting fluid will contain 0.3 per cent. of tannin. The results obtained by experiment

show that the actions of a 0.3 per cent. solution of tannin and a 5 per cent. infusion of tea-leaves closely correspond.

When tea-leaves are infused with boiling water for as short a time as two or three minutes, both the alkaloid theine and tannin are dissolved in the solution. It is a popular error that a short infusion prevents the extraction of the tannin, while permitting the solution of a sufficient quantity of the alkaloid to render the beverage of the wished-for stimulating power. In some teas, however, especially the Indian teas, which are highly fired and much fermented during preparation, long infusion causes a continued extraction of tannin after all the theine has entered into solution.

The following table, compiled from analyses made by Dittmar, shows the proportional amount of these two substances yielded by China, Ceylon, and Indian teas after infusion for five minutes and ten minutes:—

TABLE LXXV.

	Length of Infusion.			
	5 Minutes.		10 Minutes.	
	Theine.	Tannin.	Theine.	Tannin.
China	2.58	3.06	2.79	3.78
Ceylon	3.15	5.87	3.29	7.30
Indian	3.63	6.77	3.73	8.09

The table shows that Indian teas contain 25 per cent. more theine than the teas which come from China. They also contain 100 per cent. more tannin. The Indian and Ceylon teas are now more widely used in this country than the Chinese varieties, and it is obvious that, while long infusion of a China tea can yield an amount of tannin which is far less than that obtained during the course of a short infusion of Indian teas, the common practice so prevalent among the middle and lower classes of allowing the teapot to stand on the hob for hours together, with an occasional addition of fresh tea-leaves, results in the production of a fluid containing a proportion of tannin much above that capable of arresting the digestive processes in the stomach even if diluted by the presence of other fluids. The physiological action of theine consists in a stimulation of the circulation of the brain and a decrease in the sense of hunger. It "cheers but does not inebriate." It is a more valuable restorative than alcohol in long-continued and fatiguing exertion, principally because no symptoms occur of any diminution of power or of collapse of the heart or nervous system after the actual

stimulating power has passed off. In this it differs markedly from alcohol. Tea retards the action of the salivary juice upon starch and upon the pancreatic diastase. It slows the peptic digestion of proteids, but does not appear to exert much influence upon trypsin. To obviate the inhibitory effect of tea on salivary digestion a pinch of bicarbonate of soda may be added to the tea. This does not help in the extraction of the bodies contained in the leaves, but renders the infusion neutral or slightly alkaline. Tea infused for two minutes is really not inferior in stimulating qualities or in its power of retarding salivary digestion to tea infused for as long as thirty minutes, unless those varieties be used which contain a large excess of tannin. To minimise the inhibitory action of tea on digestion it should be taken in very weak solution and sparingly, and should not be drunk with, but after meals.

Coffee.—Coffee has a less marked inhibitory action on salivary digestion than tea, unless taken in the form of the French "café noir." The reason for this diminution in the power of causing retardation of digestion is found in the fact that coffee contains caffeo-tannic acid in place of tannin, a body which has less effect on digestion. Roberts found that a solution of coffee of 5 per cent. caused no slowing of the salivary digestion of starch until the coffee had been added to above 20 per cent. of the mixture, while the same proportion caused a considerable retardation of peptic digestion, its power in the stomach being almost equal to that of tea.

Coffee has little effect on any of the digestive processes carried on through the agency of the pancreatic ferments. The physiological effect of coffee is exactly similar to that of tea.

Cocoa.—Cocoa is derived from the seeds of a plant called the *Theobroma cacao*. Unlike tea or coffee, cocoa contains a large proportion, about 50 per cent., of fat, and in addition, 20 per cent. of nitrogenous material. It contains an alkaloid, theobromine, which is almost identical in composition and action with the alkaloids of tea and coffee. Cocoa, however, contains much less of this alkaloid than tea or coffee, so that when drunk as an infusion it is less stimulating; but, as its constitution shows, it is very nourishing. Most cocoas in the market have had much of their cocoa-butter extracted, and sugar, and sometimes starch, added to them. These prepared cocoas form a very nutritious food in a small bulk, and may be

advantageously taken during arduous expeditions, to serve both for food and drink.

Food accessories of the class of tea, coffee, maté, guarana, and coca act somewhat differently from one another on the muscular energy of the body. Benedicenti ascribes to all of them the power of lengthening the period before which active movements cause muscular weariness, but in various degrees. Coca acts most vigorously, both increasing and conserving muscular power; maté is the least active. Tea, coffee, and maté only cause slight actual increase of power, but enable muscular exercise to be continued for a longer time. Coffee may exercise this property for one hour after it has been taken; but tea, maté, and guarana lose their effect by the end of half-an-hour.

CHAPTER XVII.

FOODS.

Food primarily sought for Subsistence only—Habits vary with Nature of Food—Economic Changes produced by the Cultivation of Food-stuffs by Man—And by his placing a Monetary Value on them—The Ideal Food of the Future—Vegetarians—Cost of Foods and Proportional Food-values—The Food of the Working Classes—The Foods of Physiological Diets—The Food of Herbivorous Animals—The Common Food Substances used by Man—Milk—Eggs—Bread—Meats—Fruits—Fungi—The Action of Heat on Foods—Conclusion.

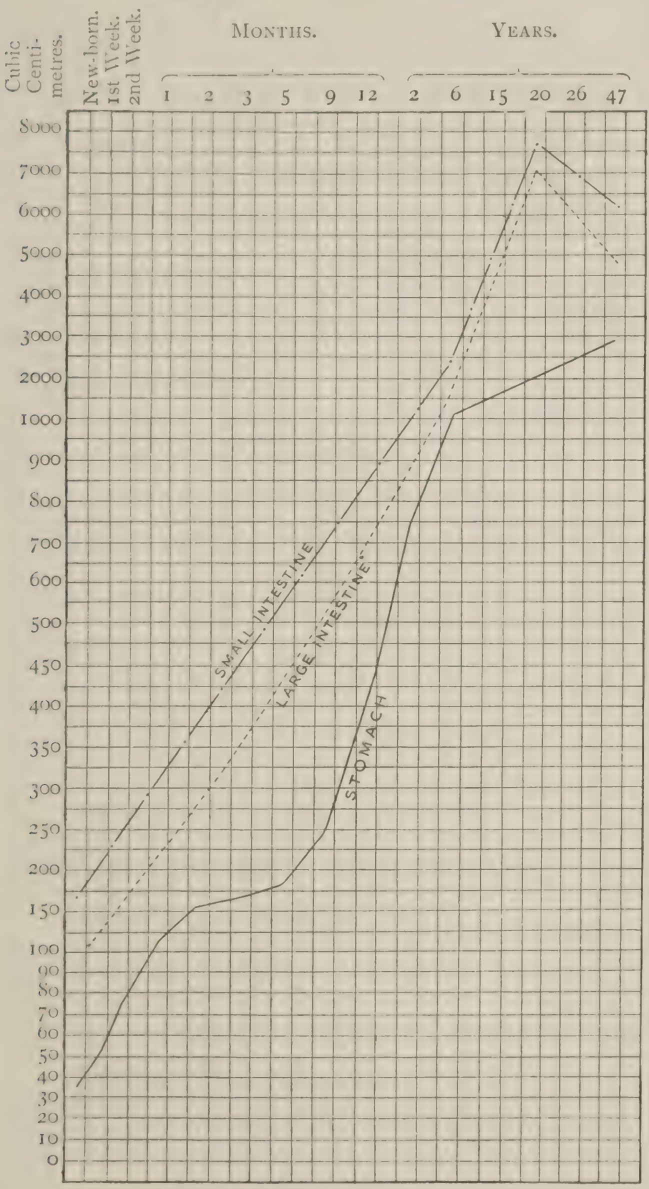
THE primary use of food is for subsistence. The plant possesses no active choice of food; if its wants cannot be supplied where the seed fell and germinated, it withers. Plants, therefore, are distributed throughout the world in absolute accordance with the possible food supply afforded by their habitat. It is true that slight variations in the composition of the soil may produce minor differences in the same species of plant, but the possible limit is circumscribed. Man has been able, through the artificial use of the necessary foods, to grow plants on soil incapable unless enriched of affording the requisite elements of nutrition; and, again, to modify their natural growth by giving them a superabundance of nutriment. Nearly all forms of animal life, on the other hand, although they may be restricted owing to their physical conformation to the use of some special class of food-stuffs, can voluntarily seek for their appropriate food. They seek it, not from any desire to eat for eating's sake, but for subsistence. When their hunger is satisfied, the search for food is suspended; when their appetite returns, they again seek for it. If the physical development of the animal is such as to necessitate the ingestion of flesh alone, the food is consumed in large bulk at one time, whenever an opportunity presents, while digestion

and assimilation are carried on at leisure. The curious circumstance of poisoning from an excess of proteid food is often exhibited by the members of the carnivora in the course of their natural habits. So in man (and here it is unnatural, save in members of savage tribes with limited opportunities for dining off flesh) an unusually large amount of meat causes sleepiness, lethargy, and mental hebetude. The *Carnivora* obtain a "subsistence-diet" from infrequent and large meals. Their food contains a greater proportion of nitrogen to carbon than the ideal 1 : 15; in reality it is as high as 1 : 5 or more, and the excess of proteid over that needed for the bodily economy has to be got rid of at the expense of a passing attack of poisoning by derivatives of the surplus proteid, formed during the process of their elimination. (Chart XXII. and Diagram VIII.)

In the vegetable kingdom the nature of the food has as much significance. A hardy plant is not only one which can resist changes of temperature, of drought or moisture, but one which can procure its food from more primitive and elementary forms than tenderer plants. A plant which can obtain sufficient nourishment from unpromising materials is hardier than one which is dependent upon special forms of food. Plants also which have developed accessory means of replenishing their larder, such as *Drosera*, *Nepenthes*, can live where others wither. In animals, the nature of the food eaten is a sure index to the character of the species. The carnivorous animal is quarrelsome, assertive; the *Herbivora* shun combats save in the rutting season, and seek by flight to avoid the attacks of enemies.

If it is asked what precautions should be taken as to diet and food, the answer may be given, "Eat what you find agrees with you, when you desire it, and how you like it cooked. Vary your diet as much as possible, and take your food in moderation, neither allowing too long a time to elapse between meals nor too short an interval. Eat slowly, and chew well. Let breakfast be the largest meal, should you be hungry enough in the morning." The stomach has had a night's rest and can digest more than in the evening, when it has had little time to recover from the day's exertions. The Continental practice of working in the early hours upon a roll and a cup of café-au-lait is not to be recommended. If you have to rise early and work before breakfast, drink a tumbler of milk

CHART XXII.—Showing the Increase in the Capacity of the Human Stomach, Small Intestine, and Large Intestine at different Ages.



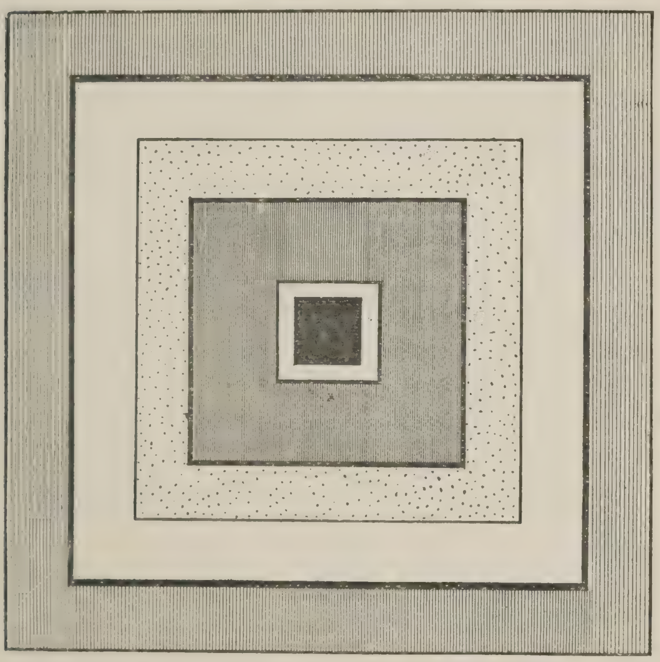
with some bread or biscuit, or a plate of porridge. Those possessed of energy enough to cause early-rising, unless necessary in the course of their employment, take more out of themselves than an early bedtime can compensate for, unless, indeed, they breakfast fully after rising and not after two or three hours fast. If early rising is accompanied by early retiring, and the meals be taken as usual but proportionately advanced in time, no harm accrues. Physical work before breakfast is perhaps not so hurtful as severe mental work, but both make use of material which has been assimilated before or during sleep, and which has not been reinforced by additional food since the last meal of the evening before. Any tissue employed for physical or mental work at a time when no reserve of material has been lately introduced, from loss of energy, and hence of its own elementary constituents, is much more prejudicially affected than if the blood could supply its needs at once. The food taken the night before is largely used in replacing the losses of the day-time; by morning the brain is refreshed by sleep, the mental powers are more active, but though seemingly more "wide-awake" and active than before sleep, the use of either brain or muscle implies the working of organs which cannot be supplied with the elements needed to replace those used up, except at the expense of other tissues. After a full meal the brain may be heavy and the muscles disinclined for work, owing to the action of the products of digestion in the blood supplying the brain, but apply the incentive of work and both brain and muscle work more powerfully, and are less soon tired.

The frequent occurrence of drowsiness and lethargy after a full mid-day meal, or a late dinner, and the almost entire absence of these symptoms after a big breakfast, indicate that Nature can cope with the digestion and the assimilation of considerable amounts of food in the morning without causing any sensible disturbance in the body, while her task on the other occasions gives evidences of its magnitude in various ways.[1]

[1] Lambinius in his notes on Plautus gives the following information as to the meals of the Romans:—"*Jentaculum* was their first meal (ἀκράτισμα of the Greeks); *Prandium* the mid-day repast, *Vesperna* the afternoon, and *Cœna* the evening meals, corresponding to the ἄριστον, ἑσπέρισμα, and δεῖπνον of the Greeks." Actuarius discussed the merits of two over only one meal in the day. Galen recommended two, Cicero only one full meal, and Haly Abbas thought a late dinner better than a large mid-day meal, thus coinciding with many authorities at the present time.

The herbivorous and ruminating animal, on the other hand, when untamed by man, usually feeds in the evening or even at night on a form of food which necessitates its ingestion in large bulk, rapidly stores this in a distended portion of the stomach

DIAGRAM VIII.—Illustrating the Capacity of the Human Stomach at Different Ages.



The central black square ($\frac{7}{20}'' \times \frac{7}{20}''$) represents 1 ounce, or 28.4 c.cm.
The small white square shows the capacity of an infant's stomach—2 ounces, or 56.8 c.cm.
The square closely shaded represents an Imperial pint—20 ounces, or 568 c.cm.
The square dotted represents the capacity in child of six years—36 ounces, or 1022.4 c.cm.
The large white square represents the ordinary capacity in adult—64 ounces, or 1817.6 c.cm.
The outer shaded square represents the ordinary capacity in adult when more fully distended —100 ounces, or 2840 c.cm.

for further masticatory treatment, and retires to pass the day in quiet rumination and sleep. In other members of the *Herbivora* the food is more finely comminuted in the mouth, while the absence of a paunch renders rumination impossible. In them the food undergoes a certain amount of digestion in the true stomach, while the processes carried on in the rumen of the first class take place in the cæcum of the second. Man, in the earliest stage of his life-history of which we have any cognisance, combined the habits of the carnivorous and of the non-ruminating herbivorous animals, except in so far as, not being in possession of either a rumen or capacious cæcum, he was unable to make use of plants rich in cellulose, which he could not digest, and whose use occasioned great irritation of the bowel. The primitive man procured the necessary nitrogen from flesh or fish, or from nuts; the carbon came from animal fats, berries, nuts, and fruits. His food, though of uncertain and precarious supply, yielded all the elements needful. Whenever he sustained life on flesh alone he was compelled to devour a much greater quantity than sufficed for the demand by his body for nitrogen; if he lived on berries and fruit an even greater excess of carbon over the physiological amount had to be consumed ere his need of nitrogen was satisfied.

If food was scanty and insufficient for all the members of the tribe or settlement to which our primitive man belonged, he fulfilled the laws of supply and demand by killing the least useful members of the community, or allowed few only of the female children born to him to survive. Such customs are still in vogue in out-of-the-way parts of the globe, even at the end of the nineteenth century. In like manner the *Carnivora* equalise the number of consumers with that of the prey by devouring members of their own order when food becomes scarce. Among plants and vegetable-eating animals the food-supply more directly influences their survival; the stronger plant ousting the weaker by appropriating the nourishment available; the stronger animal obtaining more food and eluding with greater success the attacks of enemies.

As civilisation commenced, an entirely new element influenced the laws of supply and demand. Before cultivating plants or rearing animals to act as reserves or stores of food, as well as for the purpose of physical help, man began to cook what he ate. He was very near akin to the *Anthropomorpha*, the

higher apes, until he discovered the benefits conferred by the action of fire on foods.

The day upon which a prehistoric man first sowed the seed of a vegetable in order that he might obtain from its growth a food-stuff belonging to himself marked a profound alteration in the economic value of matter. Henceforward he had conferred a fictitious value upon food-stuffs, fictitious in relation to all other commodities. Up to this time the forms of animal life were equal, their food was common property, its supply governed their habitation, their ability to secure it was their only guarantee of survival. After the prehistoric man commenced to provide artificially for his wants, no other animal species could compete with him on level terms. In time the cultivation of vegetable foods and the breeding of animals for food purposes led to the recognition of food values, and the influence of fluctuating prices for food-stuffs led to artificial variations in diet. Save in the case of those races which even now have failed to advance beyond the stage of trusting to nature for their supply of food, the prices at which the peoples of the world can afford to buy the principal articles of food, involving, of course, the actual amount of the articles available, govern the kind of food eaten by the majority. The rich and the comparatively well-to-do only vary their food to a slight extent with fluctuations in value, they curtail their luxuries and food accessories, and by so doing can afford to pay an enhanced price should the supply of any of the common food-stuffs be short. Thereby they render it impossible for the needy, who ordinarily live at the starvation point, to purchase enough food material to yield them the 18 to 20 grammes of nitrogen and the 300 grammes of carbon which are necessary to maintain good health. They may be able to obtain enough to keep body and soul together, but their food under such circumstances is very far removed from the physiological ideal. Affluence is by no means synonymous with a physiologically correct diet. The ideal condition is one under which man can just afford to provide himself and his family with an amount of food containing a slight excess of the necessary elements and no more, provided he can continue to do so under what might form adverse circumstances to others. The disadvantages of a richer diet to men of sedentary habits are counteracted by active manual employment or exercise. A farm labourer able to provide 18 grammes of

nitrogen and 300 grammes of carbon for his own consumption, with corresponding amounts for his wife and children, is fulfilling the laws of nature much more closely than the millionaire, who gluts his digestive market with food-stock unable to yield a tithe of the interest he is most in need of, although providing deferred payments in the shape of gouty or other metabolic disorders in the future; not to speak of the constant speculations indulged in by the use of champagne and other wines, speculations which afford a speedy but temporary return, followed by the inevitable "slump," and leading to bankruptcy, chronic dyspepsia, diabetes, obesity, or gout.

The ideal food of the future, so fondly dreamt of by the scientific chemist, synthetically prepared, containing the different constituents necessary for the support of the animal body in exact proportions and in very small bulk, as well as allowing of easy and rapid assimilation—such a food will never satisfy the appetite of man. An ox or a sheep is ever content to feed on grass throughout its existence. Men are so constituted that some change in their diet is essential for their well-being. It almost appears to be true that man has developed a capricious appetite, *pari passu* with the education of his higher mental faculties, to which hunger serves only for a time as the best sauce, but which requires to be titillated by different foods for its maintenance at a healthy level. To one able to procure the variations craved for, subsistence upon a single food-stuff soon becomes intolerable, while those who are so unfortunately placed as to be unable to procure other than one article of food soon exhibit evidences of malnutrition. The infant thrives on milk and on milk alone. The adult can maintain his health, and may even put on flesh, on an exclusively milk diet for some weeks or months. In the course of time, however, he begins to lose flesh, and it becomes clear that he is not procuring sufficient nourishment from the milk to keep his bodily functions at their normal level. A vegetarian may appear to be in perfect health, but his muscles are generally flabby, his power of resistance small. No human being, however, could sustain his bodily powers upon vegetables alone. He has not been supplied with either the rumen of the ox or the cæcum of the horse. A vegetarian devotee, therefore, includes eggs and milk in his dietary, basing this indulgence upon the argument that neither of these ever possessed life. In regard to milk this statement is correct, but

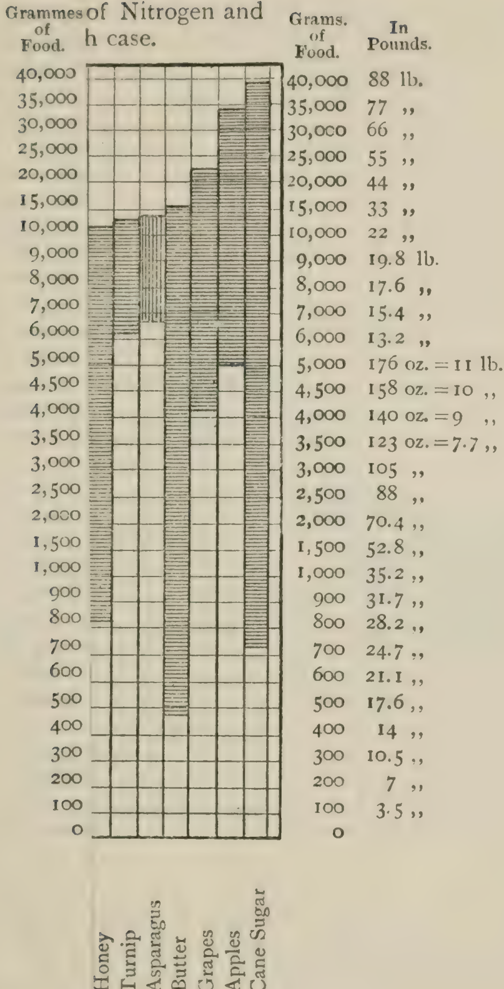
it cannot be accepted as true when eggs are concerned. An egg is endowed with life. Under favourable conditions it will develop into a living animal. Is it any more reprehensible to eat the flesh of a bird than to partake of a living germ along with the nutriment provided for it by its parent, a parent whose flesh is forbidden? Life is destroyed just as much, perhaps rather more, when an egg is eaten than when a chicken forms part of the diet. Munk and Uffelmann (*Die Ernährung der gesunden und kranken Menschen*, Wien, 1887) estimate the relation between vegetable and animal albumin, which should not be increased as far as the plant albumin is concerned, at seven to three—that is to say that no diet can be sufficient for an adult under ordinary circumstances which contains albuminous constituents derived from vegetables in a greater proportion than seven parts to every three of albumin provided by animal foods. The vegetarian follows out this law by supplying himself with animal albumin from milk and eggs, but has to eat a greater quantity of food, bulk for bulk, to obtain the other substances he requires. Man is not built to deal with the diet of a herbivorous animal; the arrangement of his alimentary canal proves his disability to cope satisfactorily with large quantities of vegetable foods.

The use of the proper food-stuffs is influenced by the very important consideration of cost. Unfortunately many persons are unable to procure those articles which serve best to supply the necessary carbon and nitrogen for the upkeep of the body, and have to content themselves with cheaper food. In Table LXXVI. details are given as to the values of some common articles of diet represented in terms of the purchasing price of one penny. These values have been calculated from the percentage composition of the food substances. The percentage figures for the nitrogenous constituents regarded as grammes have been multiplied by 5, and of the fatty bodies by 3, while those for the carbo-hydrate material have been added unaltered to the figures obtained from the first two (König). For instance, oatmeal contains about 14.5 per cent. of nitrogenous matter, 6 per cent. of fat, and 65 per cent. of starch or carbo-hydrates. Multiplying as above, we get $14.5 \times 5 = 72.5$, $6 \times 3 = 18$, and 65, which added together give the food-value of 100 grammes of oatmeal as 155.5. Lean beef in the same way $(21 \times 5 + 1.5 \times 3)$ gives 109.5. As a pound corresponds to 453.5 grammes, the food value of $1\frac{1}{2}$d. worth or a pound of oatmeal will be

TABLE LXXVI.—*The Food Values of Certain Articles of Food in Terms of Grammes obtainable for a Penny.*

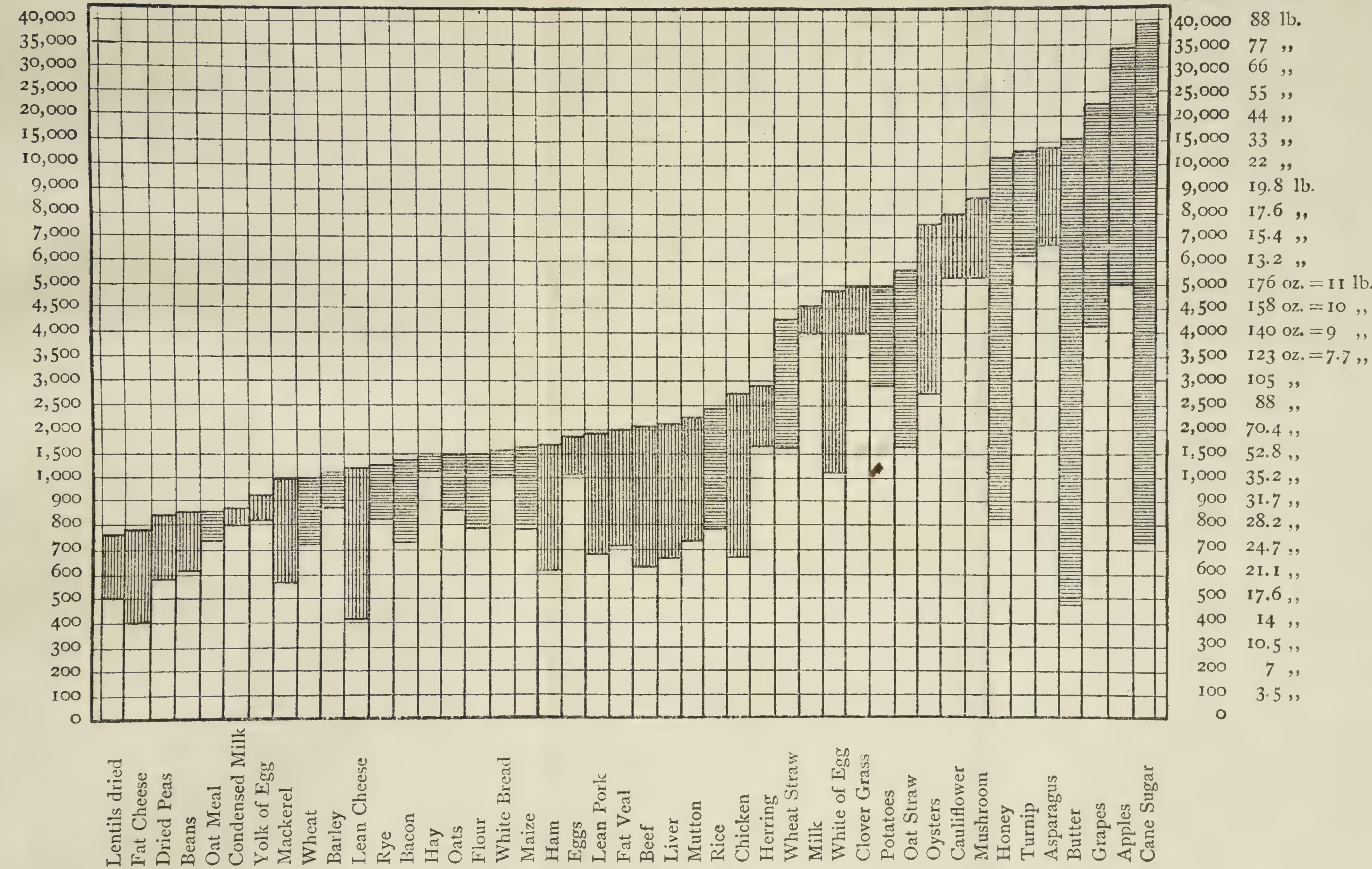
	Food Stuffs.		Cost in Pence.	Food Value obtained for each Penny.	Grammes of Nitrogen and Carbon for each Penny. Nitrogen.	Carbon.		Average number of Grammes for a Penny. Nitrogen.	Carbon.	
1. Vegetable or chiefly Carbohydrate	Sugar	453.5 grm. 1 lb.	1½	300	—	120	1.	3.73	98	(1–24.1)
	Rice	,, ,,	2	271	1.7	90				
	Potatoes	,, ,,	1¼	111	1.08	41.5				
	Oatmeal	,, ,,	1½	470	6.0	120				
	Bread	,, ,,	1½	278	3.7	78				
	Dried Beans	,, ,,	2½	317	6.25	76.21				
	Dried Peas	,, ,,	1¼	629	12.48	149.5				
	Green Peas	,, ,,	2	103	2.17	23.26				
	Apples	,, ,,	1¾	32	0.194	13.72				
2. Animal or largely Proteid.	Milk	567 cc. 1 pint	2	74	1.7	20				
	Eggs, Fresh	453.5 grm. 1 lb.	20	22.3	0.7	3.4				
	Cooking	,, ,,	8	55.9	1.8	8.2				
	Cheese	,, ,,	9	112	2.8	17.8				
	Beef, moderately fat	,, ,,	9	61.5	1.6	8.38	2.	4.0	28.0	(1–7)
	Beef, lean	,, ,,	10	49.7	1.5	6.8		Excluding Dried Cod 1.48	Excluding Dried Cod 12.6	(1–8.5)
	Dried Cod	,, ,,	2½	732	21.75	135				
	Bacon	,, ,,	12	97.5	0.17	23.7				
3. Fats.	Butter, Fresh	,, ,,	16	72	0.05	21.5	3.	0.03	33.2	(1–1106)
	Cooking	,, ,,	12	96	0.06	30				
	Olive Oil	,, ,,	7	199	—	48.1				

of Nitrogen and
h case.



The ents the number of grammes
required tion represents the number of
grammes nd thus indicates the excess of
Proteid have been reached before 20
grammes

DIAGRAM IX.—Showing the Quantities of Food-Stuffs required to yield 20 grammes of Nitrogen and 300 grammes of Carbon, and the excess of one or other element present in each case.



The figures refer to the grammes of Food required. The lower part of each column which is unshaded represents the number of grammes required to afford either 20 grammes Nitrogen or 300 grammes Carbon. When shaded with vertical lines, the addition represents the number of grammes still required after 20 grammes of Nitrogen have been provided, to complete the 300 grammes Carbon, and thus indicates the excess of Proteid in the diet. Conversely, horizontal lines indicate the excess of Carbon compounds after 300 grammes have been reached before 20 grammes Nitrogen are afforded.

$453.5 \times 155.5 \div 100$, or 705.2, or the value of the amount which can be bought for a penny is 470, while the value of a pennyworth of lean beef at 10d. a pound will be 49.7.

It is at once apparent from the figures given in the table that—(1) carbon is cheaper than nitrogen; (2) that more nitrogen can be bought for a penny when contained in vegetables than when in flesh or other animal foods; (3) that the starches and sugars are cheaper sources of carbon than fats; and (4) that carbon can be obtained at a less cost from fats and oils in the form of butter or olive oil than when bought along with flesh. Another factor, however, has to be considered, the comparative digestibility of these classes of foods. Thus, although 12.48 grammes of nitrogen contained in about 10 ounces of dried pease can be purchased for one penny, the much smaller amount present in a pennyworth of beef—1.6 grammes—is probably more easily digested and absorbed, and may serve better for the purposes of nutrition. (Diagram IX.)

Nowadays the kind of food eaten by man, as has been noted, is largely influenced by monetary considerations. A working man too often looks at the question from the point of "How much can I spend on luxuries and still leave enough for the sufficient supply of food for my household?" The wife discouraged, taught at the board-school many things, but little cooking, can only provide articles which require a minimum of preparation and afford a minimum of nourishing power. Tea and bread with tinned meats form the staple food of too many households. Fifty years ago the country labourer, although he may have had to pay a little more for his staple articles of diet, lived much more logically than his present-day successor. The food of the English labourer consisted principally of wheaten bread, cheese, and potatoes, with bacon or butcher's meat once or twice a week; the Scottish worker obtained a sufficiency of nutritive elements from milk, oatmeal, barley-bread, and, occasionally, salted fish or flesh; while the Irishman could only afford to live on potatoes, and was often unable to buy salt to eat with them. The Reports of the Poor Law Commissioners prior to 1838 contain many allusions to the food eaten by the inhabitants of Ireland about that date. The following table may prove interesting:—

TABLE LXXVII.—*The Weekly Expenditure of an Irish Labourer, with a wife and two children, receiving a wage of nine shillings per week.*

	s.	d.
Two pecks (28 lb., 12,692.4 grms.) of oatmeal at 9d.	1	6
Five pecks (70 lb., 31,730 grms.) of potatoes at 5d.	2	1
Milk (say 8 pints or 4536 c. cm.) at $1\frac{1}{2}$d. (?)	1	0
Loaf of bread (4 lb. or 1813.2 grms.)	0	6
Half-an-ounce of tea (14.17 grms.) and half-a-pound of sugar (226.6 grms.)	0	5
One pound of bacon (453.3 grms.)	0	6
Herrings or other fish (say 2 lb. or 906.6 grms.)	0	6
Coal, oil, and soap	1	$0\frac{1}{2}$
Tobacco	0	3
Rent	1	0
Total per week	8	$9\frac{1}{2}$

Per head per week, 2s. 2.375d. Per head per day, 5.2d.

About 415 grammes of nitrogen would be afforded by such a diet, allowing 20 grammes per diem for the labourer, 18 grammes for his wife, and 10.5 grammes daily for each of his children, while 9625 grammes of carbon distributed in the same proportions in the relationship of 1 gramme of nitrogen to 20 of carbon would give the labourer about 400 grammes a day, his wife about 360, and each child about 280 grammes of carbon daily. The diet is bulky and sufficient, but contains 2524 grammes of carbon in excess. The good old custom of the Scottish people in making free use of oatmeal in the form of porridge or oatcake gives one a creditable instance of their foresight in the care of their "bawbees." Porridge and milk, with perhaps a little cream added, provides the requisite proportions of nitrogen and carbon, and has the advantage of cheapness. Of late, however, the increased facility afforded to the inhabitants of the towns and the country of obtaining bread, tea, and meat is tending to cause a deterioration in the race. Porridge is thought not to be good enough, while the money spent on tea and butcher-meat leaves only enough over to provide for the cheapest of the other food-stuffs.

TABLE LXXVIII.—*Dietaries of Working Men in various Countries in* 1835.

In a "Statement of the Provision for the Poor, etc." (1835), Senior gives the following particulars, among others, of the usual food of a working man and his family in different countries :—

AMERICA.—*New York*—Tea, coffee, meat twice a day.
Massachusetts—Poultry, meat or fish, twice or thrice a day.
Mexico—Maize as porridge, or thin cakes and beans.
Columbia—Chiefly animal food.
Venezuela—Maize, vegetables, and fruit.
Uruguay—Animal food.
Hayti—Plantains, sweet potatoes and other vegetables.

EUROPE.—*Norway*—Herrings, oatmeal porridge, potatoes, oatmeal bread, bacon or salt beef twice a week, fish.
Sweden—Potatoes and salt fish in the south, porridge and rye bread in the north.
Russia—Rye bread, buck wheat, sour cabbage, soup with salt and lard.
Denmark—Rye bread, coffee, groats, potatoes, butter, cheese, and milk.
Germany—Rye bread, potatoes, meat once or twice a week, soups, beer, peas porridge.
Belgium—Bread, potatoes, milk, butter, and an occasional bit of pork.

FRANCE.—*Havre*—Meat seldom, bread, vegetables, cider, coffee, and treacle.
Marseilles—Soups, farinaceous chiefly, now and then meat soup and bouillée.
Piedmont—No meat, more maize than wheat.

GREECE.—Meat seldom, maize, bread, olives, pulse, vegetables, and salt fish.

From this table it is apparent that in the thirties only in North America could the working man afford to eat meat twice or thrice every day. In the other countries noted meat was seldom obtainable oftener than once or twice weekly. In London, at the present time, the barest subsistence diet, which is quite inadequate should hard manual labour be imperative, consists of three pounds of butcher meat and one of fat, either that on the meat or taken in the form of lard, dripping, or butter, added to which are two quartern loaves and some salt. If meat cannot be afforded, either two more loaves, or twenty-one pounds of potatoes, or about six pounds of oatmeal are consumed (Hart). Four quartern loaves and one pound of fat seem little to support life upon during a week, but they will yield 13 grammes of nitrogen and 320 grammes of carbon per diem, compared with 12.6 grammes of nitrogen and 202 grammes of carbon per diem when three pounds of meat replace the two extra quartern loaves, or 14 grammes of nitrogen and 230 grammes of carbon when six pounds of oatmeal are substituted. The influence of the cost on the available articles of diet can be well illustrated in connection with the table of the Irish labourer's weekly bill in 1835 for food on the preceding page. The rise in the price of potatoes from the figure there given to the figure at present ruling in the markets of this country amounts to the difference between $\frac{7}{20}$ths of a penny per pound and 1¼d. for the same amount, or $\frac{9}{10}$ths of a penny per pound. The cost of the weekly five pecks of potatoes would therefore be 7s. 3½d. instead of 2s. 1d., a rise of 350 per cent., and making the weekly expenditure from this cause alone 14s. instead of 8s. 9½d. Similarly, he would now pay 1½d. for each pound of oatmeal instead of $\frac{16}{25}$ths of a penny, a difference of 2s. weekly. As in its original form the cost of the food provided for four

persons was almost the lowest possible at that time, and as prices of many of the articles included have risen, a wage of 9s. a week cannot now be sufficient for the provision of an adequate food supply for four individuals.

An interesting paper by Mrs. Barnett, in the *National Review* for July 1886, contains several daily menus drawn up from experience of the working-class diet, and for their guidance in the search for the cheapest adequate diet. One of these daily menus is given below with some addenda. (Table LXXIX.)

TABLE LXXIX.—*A Daily Menu for a Labourer, his Wife, and Eight Children, in London.*

Quantity of Food.			Cost. s.	d.	Carbonaceous. Total. Carbon. Oz.	Grms.	Nitrogenous Total. Nitrogen. Oz.	Grms.
BREAKFAST—Oatmeal Porridge.								
Oatmeal -	1¼ lb.	567 grms.	0	2½	14	226	3	11.3
Tinned milk	1½ pint	850 c. cm.	0	1½	2¼	340	1	12.5
Treacle -	½ lb.	226 grms.	0	1½	7	111	—	—
DINNER—Irish Stew.								
Meat -	1¼ lb.	567 ,,	0	8	3½	88.75	3½	9.75
Potatoes -	4 ,,	1712 ,,	0	2½	14	180	2	4.82
Onions -	1¼ ,,	567 ,,	0	1	5½	34.74	1¼	1.41
Carrots -	½ ,,	226 ,,	0	1	¼	11.5	⅙	0.33
Rice -	½ ,,	226 ,,	0	1	7	41.5	½	1.08
Bread -	1½ ,,	680 ,,	0	2¼	13½	18.44	2¼	8.4
TEA—Bread and Coffee.								
Bread -	2½ lb.	1134 ,,	0	3¾	22½	307.4	3¾	14.1
Coffee -	2½ oz.	70.75 ,,	0	2½	¼	12.9	¼	1.37
Tinned milk	1½ pint	850 c. cm.	0	1½	2¼	340	1	12.5
TOTAL -	17.0 lb.	7676 grms.	2	5	92	1878.19	18½	77.56
Per individual	1.7 ,,	76.76 ,,	0	2 9	9.2	187.8	1.85	77.5
Amount obtained for one penny	9.3 oz.	26.4 ,,	0	1	3.1	64.7	0.64	2.67

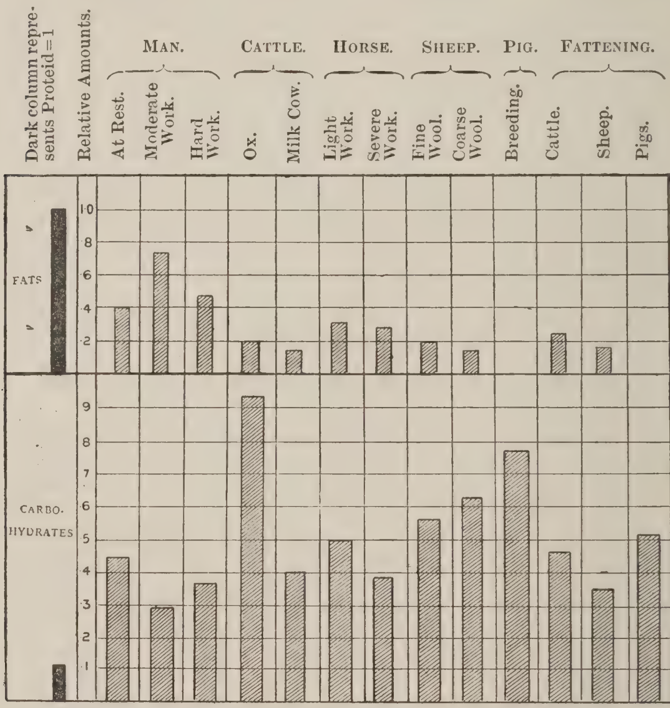
The cost therefore comes to less than 3d. a day for each—say 2½d. for each of the children, 4d. for the wife, and 5d. for the labourer. To this must be added two shillings and sixpence a week for rent and sundries, bringing the total for the week up to 19s. 5d. In the case of the Irish labourer with two children, with proportionate expenses, he would spend at least 10s. 5½d. each week, or 1s. 5½d. over his earnings. The Irishman obtained 5.1 grammes of nitrogen and 120.3 grammes of carbon in his food for each penny spent on it, but the London worker only could obtain with this menu 2.67 grammes of nitrogen and 64.7 grammes of carbon for each penny spent on food. A rise in the price of bread of as

little as one farthing for each quartern loaf, or a penny per peck of potatoes, sounds little, but means much to the poor. The price of nearly all staple articles of diet rises in sympathy with those of bread or potatoes. The question to the well-to-do or the better middle-class is only one of a change from one adequate diet to another and cheaper one; to the poorer classes it often represents inability to purchase the ordinary subsistence diet previously obtainable, and an ability to purchase food in amount or in character insufficient for their daily needs. (Diagram X.)

We have already seen that a diet, to be adequate, should contain at least 18-20 grammes of nitrogen and 300 grammes of carbon, in the relation, therefore, of one part of nitrogen to fifteen of carbon. If the diet consist solely of lean meat, the nitrogen will correspond to five times its weight only of carbon, and to procure enough of the latter, thrice the quantity of nitrogen necessary will have to be ingested. Peas and beans also contain less carbon in proportion to the nitrogen than is advisable if they form the only food taken. On the other hand, oatmeal yields 20 grammes of carbon for each gramme of nitrogen, and bread similarly yields 22 grammes. To obtain 20 grammes of nitrogen during twenty-four hours from oatmeal alone, 400 grammes of carbon require to be ingested, or 100 grammes more than needful; if bread alone be eaten, the excess of carbon reaches 140 grammes. Still more striking is the extra amount of carbon which has to be consumed by any one endeavouring to obtain sufficient nitrogen from potatoes, as 660 grammes of carbon, or an excess of 360 grammes, are necessary before 20 grammes of nitrogen are taken in. An exclusive diet of rice or of apples necessitates the consumption of 1060 grammes and 1414 grammes of carbon respectively before 20 grammes of nitrogen can be obtained from them.

DIAGRAM X.—Showing the Relative Amounts of Fats and Carbo-hydrates, as compared with Proteids, in the Diet of Man and the Domestic Animals best suited for keeping up the Body-weight.

Proteid material represented as one gramme per kilogramme of body-weight.



The columns in this Diagram are largely based on Meade Smith's data, and represent the normal proportion of fat and carbo-hydrate to proteid bodies in the food best suited for the upkeep of the body-weight, and which entails the least loss of energy required to deal with the surplus.

TABLE LXXX.—*Comparison of the Carbon and Nitrogen in Food Stuffs.*

Food-stuffs.	Amounts necessary to afford 20 grammes of Nitrogen.	Cost in Pence.	Excess or Defect of Carbon ingested in grammes. Above 300 grms.	Below 300 grms.
Beef, lean	602 grms. ($1\frac{1}{3}$ lb.)	13d.	—	230
,, moderately fat	634 ,, ($1\frac{1}{2}$ lb.)	$12\frac{1}{2}$d.	—	196
Oatmeal	1750 ,, ($2\frac{1}{5}$ lb.)	$3\frac{1}{4}$d.	100	—
Bread	1600 ,, ($3\frac{1}{2}$ lb.)	$5\frac{1}{4}$d.	140	—
Cheese	384 ,, (0.8 lb.)	$7\frac{1}{4}$d.	—	166
Potatoes	6500 ,, ($14\frac{1}{3}$ lb.)	18d.	360	—
Rice	2666 ,, ($5\frac{4}{5}$ lb.)	$11\frac{1}{2}$d.	760	—
Milk	3330 c.cm. ($5\frac{4}{5}$ pt.)	$11\frac{1}{2}$d.	—	65
Eggs	1000 grms. (2.2 lb.)	44d.	—	150
Dried Peas	606 ,, ($1\frac{1}{3}$ lb.)	$1\frac{1}{2}$d.	57	—
Butter	13,333 ,, (29 lb.)	464d.	9033	—
Dried Cod	166 ,, ($\frac{1}{3}$ lb.)	$\frac{4}{5}$d.	—	219

Illustrative diets capable of furnishing 20 grammes of nitrogen, and approximately 300 grammes of carbon, can be easily constructed from the figures given in the preceding table. The details of three theoretical dietaries are given below.

TABLE LXXXI.—*Theoretical Diets containing* 20 *Grammes of Nitrogen per Diem.*

	Articles of Diet.	Amount.	Cost.	Grammes of Nitrogen.	Grammes of Carbon.
1.	Beef, moderately fat	226 grms. ($\frac{1}{2}$ lb.)	$4\frac{1}{2}$d.	7.1	35.5
	Bread	453 ,, (1 lb.)	$1\frac{1}{2}$d.	5.7	123.0
	Milk	567 c. cm. (1 pint)	2d.	3.4	40.0
	Fat, as Butter (at 12d.)	113 grms. ($\frac{1}{4}$ lb.)	3d.	—	79.1
	Cheese	74 ,, ($\frac{1}{8}$ lb.)	1d.	3.8	25.9
	Total	1433 grms.	12d.	20.0	303.5
2.	Oatmeal	226 grms. ($\frac{1}{2}$ lb.)	$\frac{3}{4}$d.	4.52	90.4
	Milk	567 c. cm. (1 pint)	2d.	3.4	40.0
	Bacon	151 grms. ($\frac{1}{3}$ lb.)	4d.	0.68	94.8
	Eggs (Cooking)	113 ,, ($\frac{1}{4}$ lb.)	2d.	3.6	16.4
	Bread	339 ,, ($\frac{3}{4}$ lb.)	1d.	4.2	92.2
	Cheese	74 ,, ($\frac{1}{8}$ lb.)	1d.	3.8	25.9
	Total	1488 grms.	$10\frac{3}{4}$d.	20.20	359.7
3.	Milk	850 c. cm. ($1\frac{1}{2}$ pint)	3d.	5.1	60.0
	Potatoes	679 grms. ($1\frac{1}{2}$ lb.)	$1\frac{3}{4}$d.	1.81	67.5
	Butter	151 ,, ($\frac{1}{3}$ lb.)	4d	0.24	105 7
	Dried Fish	113 ,, ($\frac{1}{4}$ lb.)	$\frac{3}{5}$d.	13 56	115.0
	Total	1793 grms.	$9(\frac{6}{20})\frac{1}{4}$d.	20.71	348.2

The first of these three diets would cost a shilling a day, and would even then be just sufficient to sustain the adult body at a constant level, provided that the consumer of it did not indulge in severe bodily exertion. If the amount of nitrogen is desired to be raised, along with no great change in the amount of carbon, more meat can be given and less cheese. The second dietary scheme is largely based on substances other than flesh. It costs less, but contains an excess of carbon. The third scheme is the cheapest of the three, but the fact that the nitrogen is present for the most part in the form of dried fish renders it less agreeable and less assimilable. A sufficient quantity of nitrogen and carbon could be obtained from 1½ pound of oatmeal, 1½ pint of milk, and 1 egg (2 ounces), at a cost of only about 6¼d. It has been pointed out in a previous chapter that a diet, however fully it satisfies the theoretical conditions as to the amount of nitrogen and carbon which can be obtained from it, answers the purposes of nutrition best if the constituents be present in all the three forms—nitrogenous, starchy (or sugary), and fatty substances. A theoretically perfect diet, yielding its nitrogen from flesh and vegetable substances, and its carbon only from starch or sugar, may not be so conducive to the maintenance of bodily health as a diet containing the same quantities of these elements in which the carbon is present in fats as well as starches. Waller, in his *Human Physiology*, gives as an ideal complete diet—

Table LXXXII.—*Ideal Daily Diet.* (*Waller.*)

		Carbon.	Nitrogen.
Foundation	1.—1 pound bread ...	117 grammes ...	5.5 grammes.
	2.— ½ ,, meat ...	34 ,, ...	7.5 ,,
	3.— ¼ ,, fat ...	84 ,, ...	—
Accessories	4.—1 ,, potatoes ...	45 ,, ...	1.3 ,,
	5.— ½ pint milk ...	20 ,, ...	1.7 ,,
	6.— ¼ pound eggs ...	15 ,, ...	2.0 ,,
	7.— ⅛ ,, cheese ...	20 ,, ...	3.0 ,,
Total ...	3⅝ pounds (1324 grammes). ...	335 grammes ...	21.0 grammes.

This diet is both liberal (giving rather more nitrogen and carbon than necessary) and somewhat costly; at the current prices it would cost 14¼d. Any one accustomed to the food provided for him in a fairly well-to-do household who

compares the items which should suffice for his physiological requirements with those which he is pampered with, may well resolve to eschew much that he has been in the habit of consuming, when he realises that getting rid of the excess over the necessary quantities imposes a strain upon his organs. Most people who can afford it eat too much, too often, and too much at one time. A savage who gorges to repletion when he happens upon an abundance of food, but who probably lives upon nothing save a tightened waist-band for days between, is not an example applicable to dwellers in this country, save, unfortunately, those who do not, except at rare intervals, possess the wherewithal, from their own fault or from misfortune, to purchase enough to sustain life at a normal level. The well-to-do—including in this term all those who can afford to buy a variety of foods, especially if they be dwellers in cities, as too many are nowadays, where vitiated air, too little exercise, and deficient air cause diminished metabolic processes—are prone to eat too much, and what they do eat is often in a much too stimulating, and therefore irritating form.

The Food of Herbivorous Animals.—The various plants which serve *Herbivora* for food may be divided into three classes: *a*, plants which are nutritious in all parts; *b*, plants of which only a part may be eaten; *c*, plants which can only be eaten by certain species, acting as poisons to other animals. Many of the plants which form the sole food of the *Herbivora* are also consumed by members of the *Omnivora*. As a general rule the parts of the plant which appear above ground are most suited for animal requirements, especially during the period which elapses between early but well-commenced growth and flowering. When too young they are too watery, when they have flowered they are too dry. On the contrary, edible roots are most nutritious at a later period, after the flower has blown, when they in fact have progressed some distance towards their appointed goal, the provision for growth in the following spring. Most fruits are only edible when ripe. The bark, stems, and woody roots are more indigestible. Many animals, however, feed and thrive upon such stubborn material. The beaver, for instance, and numerous species of insects make use of it. The Red Indian in New Mexico regards the inner bark of a species of pine in the light of a delicacy, and delights to chew what must seem to others a far from delectable sweet-

meat. As has been already described, the majority of animals dependent solely upon plants for their nourishment are provided with some modification of the alimentary canal whereby they can make profitable use of cellulose, a carbo-hydrate which is absolutely indigestible by the carnivora. The food of cattle, horses, and sheep may be taken as the type of a herbivorous diet. Their foods may be divided into green and dry fodders, roots, grains and fruits, food-products, and milk. Green fodder and roots differ from the others principally in the amount of water present. Grass contains as much as 75 per cent., clover 80.2 per cent., of water, while in hay water only forms from 14 to 17.5 per cent. of the total. Turnips contain 88 per cent. of water. Green grass and clover ordinarily contain about 3.5 per cent. of vegetable albumin, 0.75 per cent. of fat, and about 8 per cent. of carbo-hydrates, 5.8 per cent. of which is in the form of cellulose. This relative nutritive value is therefore 27.75, compared with 40.61 of milk and 109.5 of beef. Clover-hay with only 16 per cent. of water affords 13.4 per cent. of albuminous matter, 3.2 per cent. of fats, and 25.4 per cent. of cellulose, corresponding to a nutritive value of 102, or almost equal to beef. The straws are much less nutritious, wheat-straw having a value of 59.1 and oat-straw of 65.7, but these values are rendered smaller in actual use from the greater difficulty experienced in digesting them.

Grasses alter much in composition in accordance with the season. Pott found that while bay grass at the beginning of May contained 27.9 per cent. of albumin, and at the end of June 12.8 per cent., in the middle of August the proportion had fallen to 7.8 per cent. During the same period the proportion of cellulose rose from 17.7 to 29.7 per cent. Young grass is therefore more nutritious than old, although containing more water, while owing to the large proportion of albumin the addition of some chopped straw to the diet is advisable. Green fodder is also more digestible than dry fodder, experiments showing that an excess of 2.7 to 3.2 per cent. of proteids, of 4.1 to 5.6 per cent. of carbo-hydrates, and of from 2.4 to 4 per cent. of fats is digested from green fodder over the amounts made use of from dry food.

TABLE LXXXIII.—*The Proportional Amounts of the Constituents of Vegetable Foods digested by the Herbivora.* (*Meade Smith.*)

	Proteids per cent.		Fats per cent.		Carbo-hydrate per cent.
Oats—Ruminants	77.3	...	82.4	...	73.7
Horses	86.0	...	77.6	...	76.3
Oat straw—Ruminants	40.7	...	30.1	...	45.5
Wheat straw ,,	27.0	...	35.0	...	44.0
Horses	36.0	...	84.0	...	24.0
Barley—Ruminants	77.0	...	100.0	...	87.0
Horses	80.3	...	42.4	...	87.3
(Hogs)	78.2	...	68.4	...	90.0
Dried Peas—Ruminants	88.0	...	74.7	...	93.3
Horses	83.0	...	69.0	...	89.0
(Hogs)	87.0	...	36.0	...	97.0
Esparcet clover—Ruminants	72.5	...	66.7	...	78.3
Meadow grass—Ruminants	70.0	...	60.0	...	73.0
Horses	69.0	...	13.4	...	66.0
Oil-cake—					
Hulled cakes—Ruminants	84.7	...	87.6	...	95.1
Unhulled cakes ,,	73.4	...	90.8	...	46.2

As a rule horses can digest more proteid but less fat and carbo-hydrate than ruminants. Horses make better use of oats than ruminants, but generally are unable to digest as great a proportion of the nutritious elements of fodder.

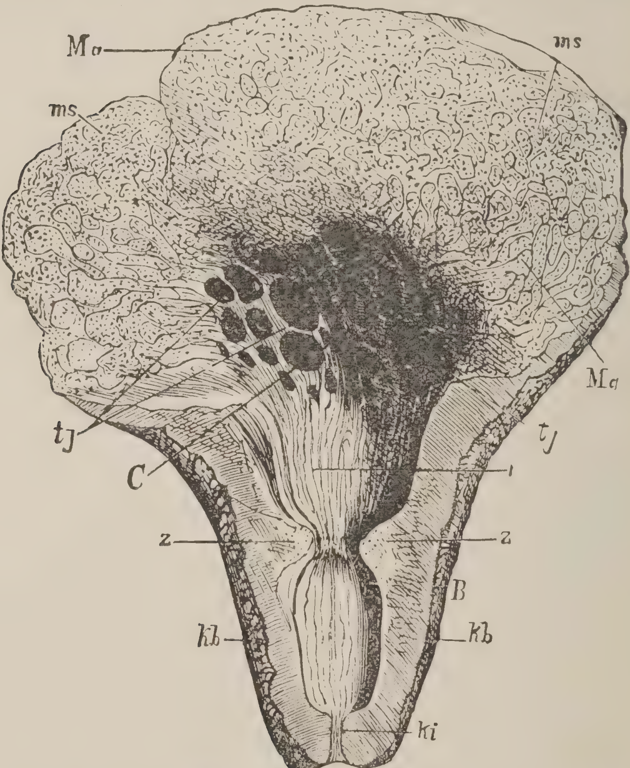
COMMON FOOD SUBSTANCES USED BY MAN.

Milk is the most digestible of all foods if consumed in a reasonable way. The sole nourishment of young animals, it contains every element required for a typical diet. Many individuals think that milk does not agree with them, "It curdles on the stomach, and becomes very acid." Such statements accord with fact, for milk should naturally curdle in the stomach. We have already seen that there is a special ferment secreted by the gastric glands for the sole purpose of curdling milk. The curds, however, which form in the stomach of the adult are usually firmer, of closer texture, and more indigestible than those in the child, owing to the addition of water in varying quantity to the child's portion. Acids curdle milk as surely as the curdling ferment, although the resulting clot is of a somewhat different character. Cow's milk forms large clots in the human stomach, and is therefore unsuited for giving to infants unless it is treated in some way or other beforehand. Human milk clots as a granular mass, similar in appearance to

that produced by the addition of acid to cow's milk. The majority of adults who believe that cow's milk is to them more or less of a poison would change their opinion were they to

FIG. 48.

THE UDDER AND NIPPLE OF THE COW (IN SECTION).



(Meade Smith, after Thanhoffer.)

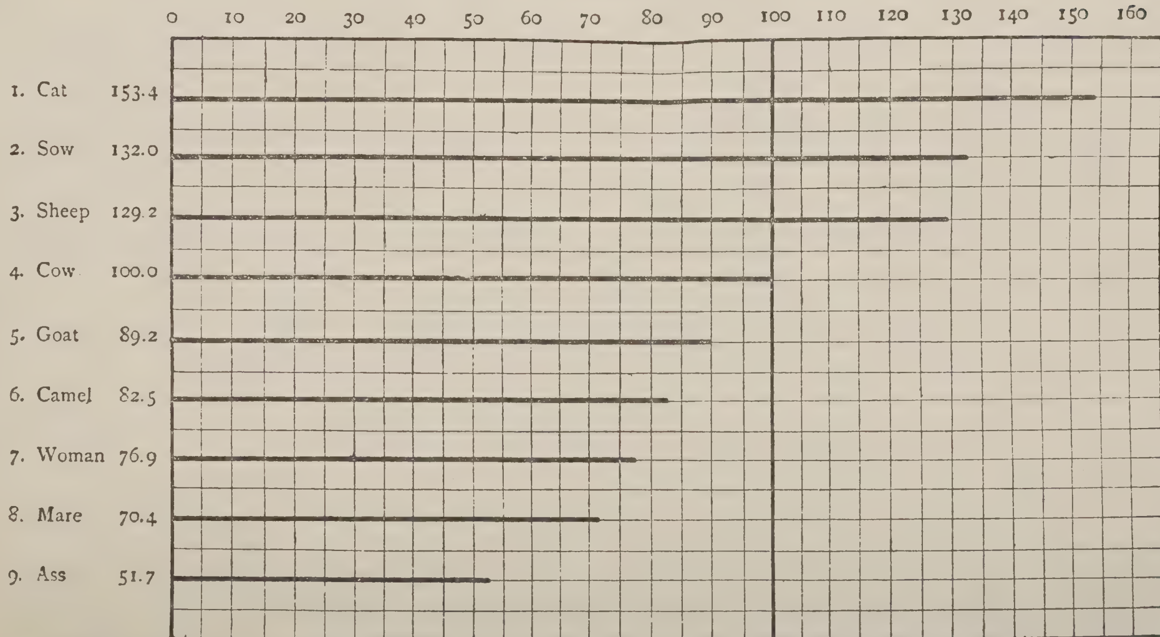
B, Nipple; *Ma*, Glandular tissue; *ms*, Acini of gland; *tj*, Milk-ducts; *C*, Milk cistern; *r*, Folds in the wider milk-ducts; *z*, Sphincter muscle; *kb*, External skin; *ki*, Milk-duct in nipple.

dilute it with lime water, or if they refrained from drinking more than a claret-glassful of pure milk at a time, in place of the tumblerful so often gulped down. The admixture of

simple aerated water to milk renders it more digestible owing to the passage of bubbles of carbonic acid gas through the fluid and the consequent softer curd. Boiled milk is more indigestible than raw milk owing to the increased toughness and density of its curd, but the process of boiling destroys any bacteria which may be present. Bacteria revel in milk—a perfect food for them—and flourish exceedingly. The addition of some phospho-carbonate of calcium (lime) will make the clot more digestible. Milk splits up in the stomach into an insoluble curd and a fluid termed the whey. The nitrogenous body originally present, a nucleo-globulin called casein, is split up into an albumose which dissolves in the whey, and an insoluble body, para-casein (Hammarsten, Maly's *Jahresbericht*, vol. ii., 1872), which forms the clot, but only if lime salts are present. Removal of all lime salts prevents the curdling of milk by ferment action. Hammarsten found that one part of the "lab-ferment" or rennet causes the curdling of at least 400,000 to 800,000 parts of casein. (Fig. 48.)

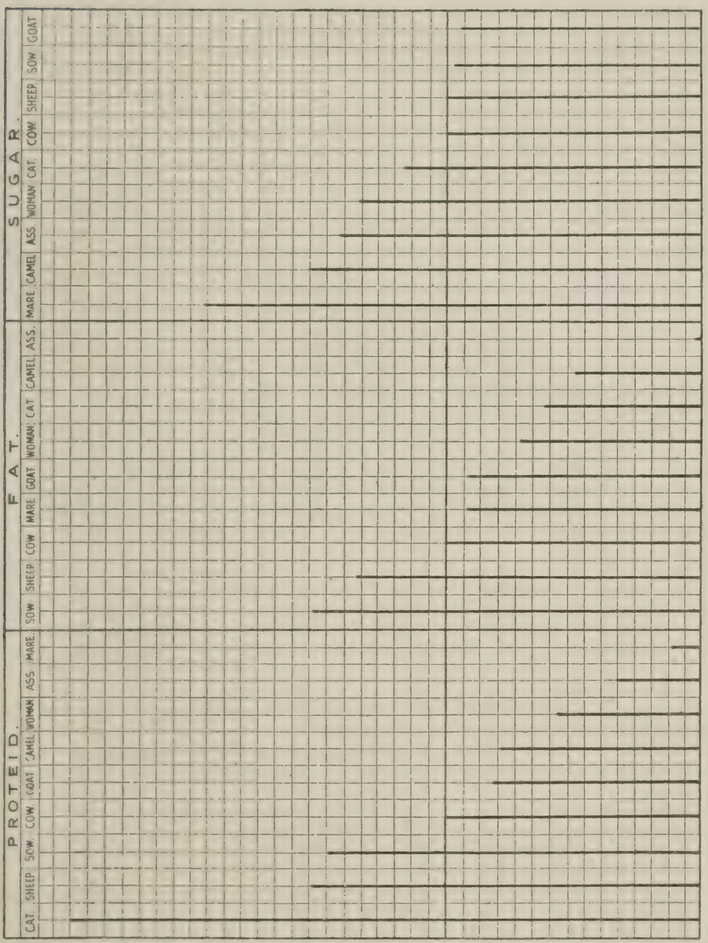
In Diagrams XI. and XII. the relations between the milk of various of the *Mammalia* are graphically shown. In Diagram XI. the nutritive value of the different milks is given as compared with that of cow's milk. It is apparent that the milk of the cat, the sow, and the sheep yield more nourishment, bulk for bulk, than cow's milk; and that human milk falls short of it, but not by so much as the milk of the mare or ass. The variations in the individual constituents of the milk of these animals, as shown in Diagram XII., also arranged in terms of the amounts present in cow's milk, are very startling. The amount of proteid in the milk of the only carnivorous mammal included—the cat—is 5.4 times greater than the amount present in mare's milk; the highest figure for fat, occurring in sow's milk, is 4.4 times that of the ass; the figures for the amount of sugar present do not show so great a divergence, the sugar of the mare's milk, the highest in value, being 1.7 : 1 compared to goat's milk. The milk of the cat owes its high nutritive value to the large proportion of proteid present in it; it is very deficient in fat, and contains a little more sugar than cow's milk. Mare's, camel's, and asses' milk afford a direct contrast to the milk of the sheep and the sow. The milk of the first series contains less proteid and fat and much more sugar than cow's milk, while the proportion of proteid and fat in the milk of the second is

DIAGRAM XI.—Representing the Nutritive Value of the Milk of various Mammals compared with Cow's Milk (= 100).



This diagram is drawn from the data in Diagram XII. The nutritive values have been calculated in terms of König's factors. The schematic arrangement is identical with that of the next diagram.

DIAGRAM XII.—Showing the Relative Proportions of Proteids, Fat, and Sugar in the Milk of various Mammals, Cow's Milk being taken as 100.



In each instance the amount of the proteid, fat, and sugar present in Cow's Milk is taken as the mean, and denoted by the figure 100; the length of each line above that figure represents the measure of the excess, the distance separating the lines which fail to reach 100, the measure of the defect of each constituent in the milk of the different animals. In each section the order is that of superior richness of the milk in the separate factor concerned.

above, the proportion of sugar below, that in cow's milk. Human milk, as compared with cow's milk, is deficient in proteid and fat but contains more sugar. When cow's milk is used for the nourishment of infants it should therefore be diluted with water and some sugar added. The sugar should be in the form of lactose or milk sugar, not of cane-sugar, as the latter is much more liable to undergo acid fermentation. The popular idea that the milk of one cow can be advantageously employed in infant feeding is incorrect. The milk of one cow is much more likely to vary in quality owing to adventitious circumstances than the mixed milk of a herd; the cow selected may be the subject of incipient disease; and, again, as the period of time which has elapsed since the dropping of a calf lengthens the milk of the cow becomes poorer. As care is taken to spread out the time of calving among the different members of a herd of milk cows the deterioration of the mixed milk from this cause is avoided. Sterilised milk, or milk heated near to but not up to the boiling point, is less dangerous than fresh milk as regards infection, and it acquires little of the pronounced taste of boiled milk, but even then it is often not relished and is not so digestible. The composition of cow's milk varies very markedly with the food given, and in connection with the manner in which the cows are kept. The following table shows the differences between the milk of cows of various breeds, and indicates that the Dutch and Breton cows give the most nutritious milk:—

TABLE LXXXIV.—*Nutritive Value of Milk from Cows of various Countries.*

	Nutritive Value.	Proteid Value.	Fat Value.	Sugar Value.
Holstein -	60.126	26.760	29.640	3.760
Brittany -	48.536	26.870	17.112	4.554
Dutch -	45.983	21.095	20.58	4.350
Durham -	45.000	21.800	19.230	3.970
Belgian -	42.252	20.100	18.660	3.292
Swiss -	38.694	12.820	21.264	4.590
Normandy -	37.597	23.665	9.720	4.212
Mean -	45.455 (3.89 per cent. Proteid, 7.3 per cent. Fat, and 4.09 per cent. Sugar).			

The milk from Holstein cows has by far the greatest quantity of cream, 9.88 per cent. (29.64 ÷ 3), the Normandy breed the least, only 3.24 per cent. The mean figures for the selected

series show an excess of fat—7.3 per cent. instead of 4.53 per cent.—over the figure given as the usual proportion of fat in milk. The Holstein and Brittany cows give a milk with much casein in it, the Swiss cows a milk which is remarkably poor in this substance. The milk of the Normandy cow is peculiar in that it contains normal quantities of proteid and sugar, but very little milk-fat.

There is a popular idea that in adults a diet of milk alone is synonymous with slow starvation. This is by no means the case. Granted that adults cannot sustain life indefinitely upon milk alone, it is nevertheless true that from five to six pints of milk drunk during the twenty-four hours provide the necessary nitrogen and only a small excess of carbon (*vide* Table LXXX.). The value of milk as a diet is clearly shown by the accompanying table (Table LXXXV.), in which the nutritive value of a pint (567 c.c.) of milk is contrasted with the nutritive values of various food articles. The values are given in terms of König's factors—*i.e.*, the amounts per cent. of proteids, fats, and carbohydrates multiplied by 5, 3, and 1 respectively and the results added together. To render the table more complete, the corresponding quantities of those foods which are necessary to yield the same amount of heat as that afforded by twenty ounces of milk are added.

TABLE LXXXV.—*A Pint of Milk*, 20 *ounces*, *corresponds in*—

Nutritive Value to				Heat Production to			
1.	3.2	ounces of	Butter	1.	1.8	ounces of	Butter
2.	3.4	,,	Cheddar Cheese	2.	2.8	,,	Cheddar Cheese
3.	3.5	,,	Ham	3.	2.9	,,	Ham
4.	4.7	,,	Beans	4.	4.3	,,	Beans
5.	7.0	,,	Hare	5.	4.8	,,	Cream
6.	7.69	,,	Beef	6.	5.7	,,	Bread
7.	8.2	,,	Cream	7.	8.3	,,	Eggs
8	8.3	,,	Eggs	8.	10.0	,,	Salmon
9.	8.9	,,	Salmon	9.	12.5	,,	Beef
10	9.5	,,	Bread	10.	12.5	,,	Hare
11.	30.0	,,	Skim Milk	11.	15.0	,,	Potatoes
12.	30.0	,,	Oysters	12.	26.0	,,	Beer
13.	32.0	,,	Potatoes	13.	28.0	,,	Skim Milk
14.	36.0	,,	Butter Milk	14.	36.0	,,	Butter Milk
15.	42.0	,,	Beer	15.	54.0	,,	Oysters
16.	84.0	,,	Whey	16.	70.0	,,	Whey
17.	86.0	,,	Strawberries	17.	128.0	,,	Strawberries
18.	203.0	,,	Beef Tea	18.	200.0	,,	Beef Tea
19.	(6.6?	,,	Whisky)	19.	3.7	,,	Whisky

It will be seen that in nutritive value a pint of milk is equal to, among other foods, 7.69 ounces of beef, 8.3 ounces of eggs, 3.4 ounces of cheese, 30 ounces of oysters, 32 ounces of potatoes, 42 ounces of beer, and 203 ounces of beef-tea; while the combustion in the body of 20 ounces of milk affords as much heat, everything being equal and the combustion complete, as 1.8 ounces of butter, 2.9 ounces of ham, 5.7 ounces of bread, 12.5 ounces of beef, 128 ounces of strawberries, and 3.7 ounces of whisky. It must be kept in mind in this connection that the nutritive value of foods and their relative power of yielding energy by combustion do not run parallel with the foods required by the body. Butter, for instance, affords a large number of heat-calories when oxidised, but no one can live on it alone. The ease with which the different foods mentioned can be digested, and the proportion of their elements absorbed, also complicate the question. It would take up too much space to correct the figures given by the factors for their digestibility. Of the casein in milk 92 per cent. is absorbed, all of the sugar, and 95 per cent. of the fat, so that practically all of the chief constituents of milk are made use of under ordinary circumstances. On the other hand, only 75 per cent. of the small proportion of albumin in the potato is digested, and 93.5 per cent. of its starch.

Eggs.—The average weight of a hen's egg is 51.1 grammes, or nearly 2 ounces, 11.9 per cent. of which consists of shell, 55 per cent. of white, and 33.1 per cent. of yolk. The white is composed of egg-albumin dissolved in water and surrounded by a delicate membrane lining the inside of the shell. The yolk contains fats, olein, palmitin, cholesterin, and lecithin (cf. p. 149), extractives, sugar and salts, much phosphorus, sulphur, and iron. The fresher the egg is, the more nutriment does it contain; the more completely cooked, the more indigestible does it become. Raw eggs are easily digested, soft-boiled or poached eggs less so, while hard-boiled or fried eggs take longer to quit the stomach than any other food which has been hitherto tested save salt-pork and cabbage. Raw eggs remain 2 hours, soft-boiled 3 hours, and hard-boiled eggs 5 hours in the stomach. To obtain a boiled egg in perfection the usual method of placing it in boiling water or steam for a short period is faulty. Whenever the white of the egg next the shell becomes heated above 73° to 75° Cent. it coagulates and prevents the ready passage of heat to the parts within. When very fresh

the white within the shell is often coagulated with difficulty, it rather becomes creamy. The same condition may be brought about by cooking eggs not so newly laid in water kept at or about 73° Cent. (163° Fahr.) for a considerable time, whereby the heat penetrates the egg substance equally, when raising the temperature of the water for a brief period will give a soft-boiled and creamy character to it. As the albumin or white of egg, in solution, does not coagulate on boiling in the absence of an appreciable proportion of neutral salts in the water, the addition of some common salt in poaching eggs is desirable. When the white is in a concentrated form, however, as in the egg itself, coagulation occurs. The composition of, and other details about, the white and yolk of eggs are tabulated below.

TABLE LXXXVI.—*The Composition and Nutritive Value of Hen's Eggs.*

	Water.	Proteid.	Fat.	Carbo-hydrate.	Nutritive Value.
Yolk	50.82	16.24	31.75	0.13	176.68
White	85.75	12.67	0.25	—	64.10
Total Egg ...	73.67	12.55	12.11	0.55	99.63

6.2 oz. of yolk, 17 oz. of white, or 10.9 oz. of total egg equal 10 oz. of lean beef. One hen's egg of 2 oz. corresponds to 1.8 oz. of beef.

The table shows that the yolk is vastly more nutritious than the white, while the total nutritive value of an egg is very slightly below that of beef. The amount of energy obtainable from an egg is greater than that of lean beef owing to the greater proportion of fat present, 163 calories to 101 calories.

Breads.—The "staff of life" can only be properly made from wheat and rye, owing to the presence in these cereals of a nitrogenous body, gluten, which enables wheat and rye flour to be kneaded with water into a tenacious (glutinous) dough. This dough is divided into two portions, one twice the size of the other. To the larger portion salt is added, to the smaller the ferment, yeast. The "leavened" dough is set aside in a warm place until it has become porous, owing to the production of carbonic acid by the action of the yeast on the sugar present in it. It is then thoroughly mixed with the larger portion set aside beforehand, the whole allowed to ferment until the risen mass tends to sink again. It is then fired in an oven. The changes which occur during fermentation consist of a

partial change of starch into dextrin and sugar, and of sugar into carbonic acid gas and alcohol. The action of heat changes much of the starch into dextrins, especially in the crust, while the previously soluble albumins are rendered insoluble. The process of "raising" bread by the action of fermentation has now been largely supplemented by the chemical formation of carbonic acid in the dough from the reaction between bicarbonate of sodium and tartaric acid, or by forcing carbonic acid gas into the dough under pressure. New bread to some persons is indigestible, but it has the advantage over older bread of being practically free of germs. Rusks are pieces of bread slowly baked until all the starch has changed into dextrins, while biscuits are forms of unleavened bread toasted until the same change has occurred.

Bread made from fine flour contains less albumin and more starch and sugar than bread made from coarser varieties. Whole meal bread gives a much higher percentage of proteids, a slight increase of fat, and a lower proportion of starch and sugar. The digestion of whole meal bread, however, is not so complete, and there is a much greater quantity excreted unchanged than in the case of white bread. The composition of bread-stuffs, along with their additional merit of cheapness, render them of great value for food; and, as bread forms the larger part of the food of the working classes, especially of those resident in towns, it is a matter of great importance that it should be made in such a way and of such materials as to render it as nourishing as possible. About 60 ounces of moist bread will yield sufficient nitrogen, and more than double the quantity of carbon necessary for the daily wants of the body, but it affords far too little fat. The addition of milk will remove the greater part of these defects, and with some ham, bacon, or salt fish will serve to form a correct diet.

Meats.—The muscular tissue of animal bodies forms the class of foods known as meats. Along with the muscle fibres are the nerves, blood-vessels, and connective tissue which serve in life to nourish and support them, and, what is still more important, a greater or less amount of blood. The proportions between the various constituents of meat are greatly altered by the presence or absence of fat and blood in the muscle. Blood is usually drained off as freely as possible before a carcase is cut up; in veal, indeed, the blood is almost completely removed. Absence of blood renders

the flesh paler, more delicate, and less liable to decompose. When an animal has been killed, after a variable period, dependent upon the mode of death and condition of the body, all the muscles become stiff. This is the result of a change in one of the proteids of the muscle fibre. During life this proteid is supposed to be present in the form of myosinogen, which is altered into myosin upon the setting free in the muscle substance of a ferment akin to that causing coagulation of the blood. However it may be caused, the alkaline reaction of living muscle becomes acid. Meat is seldom eaten until this *rigor mortis* or stiffening has passed off As the characteristic proteid of muscle or myosin belongs to the class of globulins, it is insoluble in pure cold water (cf. p. 145), but is slowly and partly dissolved in dilute salt solutions. Cold water extracts of flesh therefore can abstract no myosin, and will contain only about 2 to 3 per cent. of soluble albumin of the blood in the meat. If salt be added some of the myosin may be dissolved out of the meat, but the maximum proteid strength of a watery solution of meat can never be high. Whenever the water is heated above the point at which proteids coagulate, no further extraction of albumins or globulins can occur. A temperature of from 70° to 80° Centigrade (158°-176° Fahr.) will suffice to coagulate most proteids, if there be some salt in the water round them or in their substance. Once they have coagulated they are absolutely insoluble in water, and may be boiled indefinitely without the extraction of any further proteid.

The flesh of young animals is more tender and sometimes more digestible than of full-grown beasts, but it is not necessarily more nutritious for those reasons. Veal is less nutritious than beef, lamb than mutton. Salted or pickled beef and mutton are rendered less digestible, while ham, tongue, and bacon are more easily digested in the cured state than when used in a natural condition. Figures in connection with the theoretical nutritious value of different meats, the time taken for their digestion in the stomach, and the quantities of each required to afford as much nutriment as 10 ounces of lean beef, are given in Table LXXXVII.

The value of fat beef is seen to be high, that of lean beef less than of many other forms of flesh-food. Bacon and ham head the list, excluding beef powder as an artificial product; only 4.2 ounces of bacon or 4.5 ounces of ham are necessary

to supply the same amount of nourishment as 10 ounces of lean beef. Lean mutton, and veal, and kidneys contain less nutriment than lean beef. Fat beef, however, is more nutritious than the majority of the other meats. Beef-tea is credited with only 0.5 per cent. both of proteid and of fat, giving a value far below that of beef, and rendering the absorption of 274 ounces necessary before the same amount of nourishment contained in 10 ounces of lean beef is equalled. With only 0.5 per cent. of proteid, which is equal to 0.08 per cent. of nitrogen, no less than 5.5 gallons, or 25 litres, would be required before 20 grains of nitrogen could be supplied to the body.

TABLE LXXXVII.—*The Nutritive Value, per cent., Digestibility, and Comparative Value of certain Meats.*

	Nutritive Value.	Duration of stay in stomach before complete digestion or removal.	Amount of each, equal to 10 oz. of lean beef.
Beef (fat)	165.09 ...	Steak, 3 hrs.	... 6.6 oz.
,, (lean)	109.50 ...	,, 1hr. 30m. to 5hrs. 30m.	... 10 oz.
Mutton (fat)	183.17 ...	Stewed, 3 hrs.	... 6.2 oz.
,, (lean)	102.80 ...		... 10.6 oz.
Veal (fat)	116.62 ...	Roasted, 4 hrs.	... 9.4 oz.
,, (lean)	101.66 ...		... 10.7 oz.
Pork (fat)	184.72 ...	Boiled, 2hrs. 30m.	... 5.8 oz.
,, (lean)	121.68 ...	Roasted, 4 hrs.	... 9.0 oz.
Ham	240.79 ...	Boiled, 3 hrs.	... 4.5 oz.
Game	118.00 ...	Roasted, 4hrs. 30m.	... 9.3 oz.
Hare	120.29 ...	......	... 9.1 oz.
Chicken	113.00 ...	2 to 4 hrs.	... 9.7 oz.
Liver	117.69 ...	Roasted, 2 hrs. Raw, 2hrs. 15m.	... 9.4 oz.
Tripe	115.20 ...	Roasted, 1 hr.	... 9.5 oz.
Sheep's Kidney	91.00 ...	......	... 12.0 oz.
Sweetbread	113 00 ...	......	... 9.7 oz.
Bacon	256.50 ...	Fried (lean) 3 hrs. (fat) 4 hrs.	... 4.2 oz.
Tongue	123.50 ...	......	... 8.9 oz.
Powdered Meat	380.00 ...	......	... 2.9 oz.
Beef Tea	4.00 ...	... ..	...274.0 oz.
Liebig's Extract of Meat	3.03 ...	... ..	...361.0 oz.
Bovril	127.51 ...	......	... 8.6 oz.

The nutritive values are given in terms of König's factors, already mentioned (cf. p. 369), the duration of the stay in the stomach from Beaumont's researches.

The flesh of fish, considered in the same way, as depicted in Table LXXXVIII., is in many instances of less value, weight for weight, than lean beef, but mackerel, sprats, shell-fish, salt herring, and especially dried cod, yield higher values. The calculated nutriment in 10 ounces of lean beef, supposing complete combustion in the body to occur, is contained in only 2.7 ounces of dried cod, while 42.3 ounces of oysters are necessary to give the same amount, or about five dozen of these bivalves, while twelve dozen would suffice to supply 20 grammes of nitrogen. The flesh of white fish is more easily digested than ordinary butcher-meat, chiefly because of the absence of fat. The flesh of oily fish is not so digestible, but has a much greater nutritive value, a value which is much enhanced when the relative prices are taken into account.

TABLE LXXXVIII.—*The Nutritive Value and Digestibility of the Flesh of certain Fishes and Shell-fishes, and their Value compared with Lean Beef.*

	Nutritive Value.	Duration of stay in stomach.	Amounts equal in value to 10 oz. of lean beef.
White Fish	99.20	Boiled, 3 hrs.	11.0 oz.
Mackerel	137.78	......	8.3 oz.
Herring (fresh)	71.88	......	15.0 oz.
Salt Herring	149.00	......	7.6 oz.
Salmon	97.16	Boiled, 3 hrs.	11.2 oz.
Sole	60.45	Boiled, 3 hrs.	18.0 oz.
Eel	89.90	......	11.9 oz.
Pike	94.75	......	10.5 oz.
Sprats	163 00	......	6 9 oz.
Dried Cod	403.00	Boiled, 2 hrs.	2.7 oz.
Caviar	196.80	......	5.5 oz.
Oysters	25.86	{ Raw, 3 hrs. Cooked, 3hrs. 30m.	42.3 oz. (58 oysters)
Shell-fish (mean)	113.47	......	9.7 oz.

Fruits.—Fruits possess very varying food-values; most of those growing in this country are of little use for nutrition, and consist of little more than flavoured water. The most valuable constituents of fruits are their acids, which cannot serve as food, but which appear to be most beneficial to metabolic processes generally. The grape contains the least water, with 78 per cent.; the strawberry, with 87 per cent., the most.

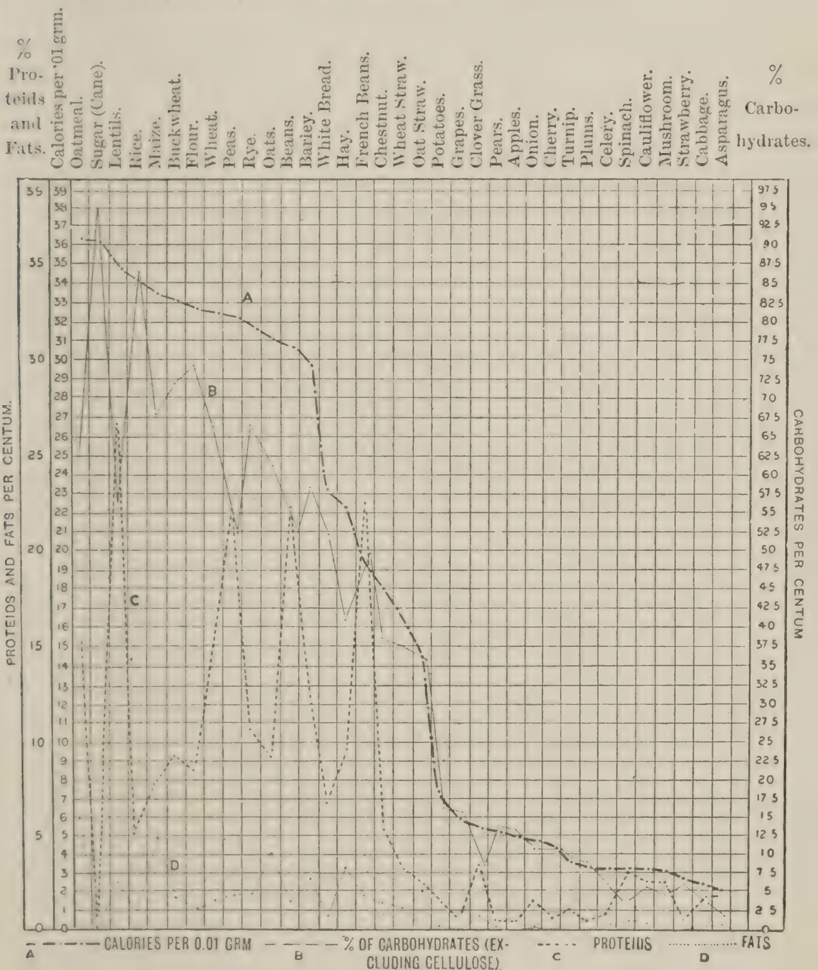
TABLE LXXXIX.—*The Percentage of Water and Nutritious Elements in certain Fruits.*

Fruit.	Water.	Proteid.	Fat.	Free Acid.	Sugar.	Nutritive Value. (Carbo-hydrates other than Sugar not included.)
Fresh						
Apple	83.58	0.39	—	0.84	7.96	9.91
Pear	83.03	0 36	—	0.20	8.78	10.58
Plum	81.18	0.37	—	1.50	6.44	8.29
Cherry	80.26	0.82	—	0.91	11.72	15.82
Peach	80.03	0.65	—	0.92	4.48	7.73
Strawberry	87.66	1.07	0 45	0.93	6.28	12.98
Apricot	81.22	0.49	—	1.16	4.69	7.14
Damson	81.18	0.78	—	0.85	6.15	10.05
Grape	78.17	0.59	—	0.79	14.36	17.31
Gooseberry	85.74	0 47	—	1.42	7.03	9.38
Greengage	80.28	0.41	—	0.91	3.16	5.21
Orange Pulp	89.01	0.73	—	2.44	4.59	8.24
Dried						
Apple	32.42	1.06	—	2.68	41.61	46.64
Pear	29.41	2.07	0.35	0.84	29.13	40.53
Damson	29.83	2.55	0 53	2.77	42.65	56.99
Cherry	49.88	2.07	0 30	—	31.22	42.47
Grape	32.02	2.42	0.59	—	54.56	68.43
Fig	32.21	5.06	—	—	45.28	70.58
Nuts, etc.					Sugar and other non-nitrogenous bodies.	Including other Carbo-hydrates.
Almonds (Sweet)	5.39	24.18	53.68	—	7.23	289.17
Walnut	4.68	16.37	62.86	—	7.89	277.32
Hazel-nut	3.77	15.62	66.47	—	9.03	286.54
Fresh Chestnut	51.48	5.48	1.37	—	38.34	69.85

It is at once apparent that the nutritive value of even dried fruits, except of those which may be classed as nuts, is very low. The banana, which is not included in the table, is much more nutritious than the greater majority of fruits. Three dozen are reckoned as equivalent in value to a week's supply of white bread. The pine-apple and the fig contain active digestive ferments, and are therefore more digestible than might be anticipated. The juice and soft parts of the pine-apple are easily tolerated if the fruit be ripe, even by those of weak digestion. (Chart XXIII.)

Fungi.—A number of the fungi are edible but only a few species are eaten, owing to fear of the evil results which follow

CHART XXIII.—Giving the Heat Calories per 0.01 gramme of different Vegetables, Grasses, and Fruit, and the Percentages of Proteids, Carbo-hydrates, and Fat contained in them.



the use of poisonous members of the order. Fungi are more nutritious than fresh fruit, but it is doubtful if the proteid in them is digested to any great extent, while the amount by weight of fungi which can be safely taken is so small compared with the total requirements of the body that they can never form an important item in diets.

TABLE XC.—*The Composition of Mushrooms and Truffles.*

		Water.	Proteid.	Fat.	Sugar and Cellulose.	Nutritive Value.
Mushrooms	Fresh	91.11	4.68	0.40	3.45	28.05
	Dry	17.54	23.84	1.21	34.56	157.39
Truffles -	Black	72.00	8.78	0.56	16.59	62.17
	White	72.34	9.96	0.44	15.16	66.28

Sugar is present as dextrose and mannite in these fungi. The truffle is found in two forms, the black and the white truffle. The black variety is esteemed for its flavour over the white, but both are extremely indigestible. A lichen, *Cetraria islandica,* or Iceland moss, is given as a food to convalescent patients or to those who are unable to tolerate the ordinary articles of sick-room cookery. A decoction of Iceland moss forms a soft jelly on cooling. *Cetraria* contains when dried 70 per cent. of a peculiar starch, lichenin or lichen-starch, which is capable of affording nourishment. The name Iceland moss is a misnomer, the plant being actually a seaweed or lichen.

THE ACTION OF HEAT ON FOODS.

Man, as has been said, is a cooking animal, and the statement is true of practically the whole human race. Only a few savage tribes remain who do not find it absolutely necessary to subject their food to the action of heat before eating it. Cooking fulfils several functions. The first is one which the man who discovered and began to practise the art, in a manner which doubtless would dismay our present-day sybarites, can scarcely have realised, that is the avoidance of the unnecessary exertion implied by the body being compelled to expend some of its heat in warming the food supplied to it. Secondly, cooking softens many hard tissues and hardens many tough tissues, rendering the first soft enough, the latter brittle enough, for the purposes of thorough mastication. Again, many chemical changes are brought about.

Almost everything expands on heating, and in foods this expansion renders them more porous, and if boiled allows thorough permeation of their substance with water. Starch grains swell and burst their envelopes, cells of all kinds absorb water by imbibition. Connective tissue is altered in part to gelatin; albumins, save the legumin present in many vegetables, are coagulated; fats rendered fluid, and some of the starch changed into dextrins. In addition, heat causes the development both in meat and in vegetables of complex substances which serve to flavour them. Raw meat and raw cabbage have practically no smell, but when cooked give off very characteristic volatile, odorous particles which serve, as has been pointed out, to give a flavour to the food quite apart from the actual taste. Another result of thorough cooking, by which man empirically forestalled the discoveries of later centuries, lies in the destruction of all micro-organisms or parasites in the food. Even now wherever the custom prevails of eating some forms of meat in an uncooked state, as, for instance, raw ham in Germany, parasites are frequently taken in with the food in a living condition and produce disease in the body of the consumer. The *Trichina spiralis* not uncommonly is the cause of disease in Germany, here it is practically unknown. Similarly, a greater number of animals suffer from intestinal parasites than man, because the uncooked state of their food permits larvæ to enter their alimentary canal with their vitality unimpaired. The successful passage of larvæ through the acid digestive fluid of the stomach is rendered possible by the indigestible nature of their outer covering. The disadvantages attendant upon the action of heat upon food-stuffs are few and of small consequence when compared with the advantages which have just been detailed. Several articles of diet are more easily digested before cooking than after it. Raw meat, if pounded to break down the outer more indigestible part of the muscle-fibres, is more easily digested than when cooked. Raw eggs and raw milk are similarly more digestible than when boiled.

All methods of cooking may be divided into two classes. The one class aims at the retention of all the juices of the meat or vegetable within the food itself; the other seeks to abstract the juices. The simpler the method, the more easily digested is the food. Few cooks properly understand the rationale of the various forms of treating food by heat. The

cardinal factor in most cases is the coagulation of albumin at a temperature much below the boiling point. The actual object aimed at is the adequate heating of the food material in all parts; the usual result obtained is an excessive heating of the outer portion, with a deficient heating of the interior. In roasting meat it should be placed close to the fire for a brief period, about eight minutes, until the outer albumin has firmly coagulated, and formed a skin which can retain the juices of the inner portion. Then the meat should be removed to a greater distance from the fire, where it becomes heated through at a lower temperature without cracking the surface skin of coagulated albumin. Even when the temperature to which meat is exposed is much above 100° Cent., the temperature of the inner portion seldom rises much above the coagulation point of albumin. If the process of roasting be properly carried out, the longer period during which the meat is exposed to a lower temperature suffices to destroy any organisms or parasites present as effectually as exposure to a higher temperature for a shorter time. Most of the constituents of meat should therefore remain *in situ* when it is properly roasted, and this mode of cooking should result in a minimum of loss. Even here the loss of weight by evaporation of water reaches to 25 per cent., or as much as a quarter of the original total. Baking is the same process as roasting but performed in an oven, and produces the same result; indeed, on the Continent meat is invariably roasted in the oven, not before the fire, and many good authorities pronounce it to be the better plan. Broiling is only a variant of roasting, in which the meat is cooked over the fire not before it, and the same results are obtained by it. Roast, baked, and broiled meats are characterised by their delicate though very perceptible flavour and odour occasioned by the retention of much of the fat or oil in the meat, and by the chemical decomposition of some of the fat of the external parts through the agency of direct heat. In boiling meat, also, a skin or outer layer of coagulated albumin is indispensable for the retention of the soluble parts of the meat. The water should therefore be boiling actively before the meat is put in. A coating of coagulated insoluble albumin at once forms round the meat, and this may be hastened by adding some common salt to the water before putting the meat in, and thereby raising the temperature at which the water boils (Knight). In a short time the outer skin has formed, when the

temperature of the water should be lowered to just above 75° Cent. (167° Fahr.), and kept at that point. Knight recommends the addition of three pints of cold water for every gallon whenever the liquid boils. Cooking by boiling is usually practised at too high a temperature, and results in the progressive coagulation of the proteids from the outside inwards. Properly an insoluble skin should first be formed, and then the whole joint raised to an equal temperature close to the coagulation point, while it may be afterwards subjected to greater heat for a brief period. Treatment of the meat with water at the boiling point throughout the process overcooks the outer part before the inner part has had time to become sufficiently warmed. In spite of all precautions, a considerable loss of the soluble part of the meat occurs in the process of boiling, but the loss is chiefly made up of extractive matter which is not in itself a source of nutriment. Cooking vegetables by steam instead of by boiling them in water is based upon sound scientific principles. The proteid constituents of vegetables are frequently soluble in boiling water, as also is the case with much of their carbohydrate moiety. Hence to boil vegetables and then to throw away the water is simply wasting much of their useful constituents. Many vegetables are valued as much for the salts and acids contained in them as for the common food-stuffs. The water in which they are boiled contains the greater part of these salts and acids. If cooked by steam under pressure, the heat applied to them is sufficient to burst the envelopes of the starch grains and to soften the cellulose, without occasioning any appreciable loss of soluble matters.

The vexed question of the nutritive value of beef-tea and soups is too complicated for complete discussion here. It has been stated on page 391 above that the chief proteid of flesh is insoluble in pure water, and that only about 2 per cent. of albumin, soluble in cold water, and derived from the blood, is present in meat. Beef-tea, made by plunging a portion of lean beef into boiling water and cooking it for some time, affords a fluid, after removal of the beef, about as nourishing as the water in which an egg has been poached. If made by prolonged soaking in tepid water and by gradually raising the temperature, beef-tea contains a little more proteid, but the proteid cannot be in greater proportion than is represented by the 2 per cent. of soluble albumin in the beef, dissolved in an excess of water. Beef-tea, however, made from pounded beef

soaked in a little water, cold or tepid, to which 10 parts of salt have been added to every 100 of water, strained, more water added, and the solution then heated to the boiling point, will contain much of the albuminous material coagulated in a fine form throughout the fluid, in addition to all the ordinary constituents of the usual beef-tea. The term beef-tea is a singularly accurate one. Tea is not nutritious, it is merely a nerve stimulant. Beef-tea, as commonly made, is likewise a stimulant, and by no means a food.

Many of the meat extracts in the market are practically solutions of beef-tea concentrated to a syrup or to a paste. Consequently they are devoid of any great value as foods, but act well in many cases as a food accessory or stimulant. They consist largely of extractive bodies. The digestion of proteids is rendered more complete and is facilitated by the presence of extractives, partly no doubt through the stimulation of the appetite by their physical properties, their odour and taste, partly by direct stimulation of the gastric mucous membrane. They do more good than harm, but the commercial preparations believed to be foods, but chiefly formed of extractives, should not command so high a price as they do in virtue of their supposed nutritive value. Some of the meat preparations, on the other hand, are really foods of great value. Often this value depends, not so much upon the actual proportionate nutritive value compared with that of beef, as upon the ease with which the proteids (present in a fine state of division) can be digested and absorbed, and upon the small space which the extract occupies. In several of the preparations lately offered to the public a greater or less part of the albumin is predigested, rendering absorption still more rapid and the preparations of greater utility.

Frying ought simply to be boiling in oil in place of water. The oil may be provided by the food itself, as for instance by herrings and sausages, or may have to be added. Fried food is strongly flavoured, and is easily made unpalatable by the presence of the products of fat decomposition. Stewing aims at cooking the food in a strong solution of its own juices, and should be carried on at a low temperature until close upon the time for serving, when the temperature should be quickly raised. Stewing and, provided the bouillon and bouillée are both made use of, boiling are the most economical methods of cooking food, nothing being lost.

Soups from which all the coagulated albumin has been removed, and which contain no vegetables, are no more nutritious than beef-tea. If made in the same way as has been recommended in the case of beef-tea, at a low temperature, with finely cut or minced meat, soup is of more value as a food. When a soup is intended to afford nourishment derived both from animal and from vegetable articles of food, the vegetables used require to be subjected separately to a higher temperature beforehand to soften them. They may then be added to the cooler meat soup.

The dilution of the contents of the stomach with fluids during active digestion tends to retard the processes in that organ. The percentage of acid present is diminished, the quantity of fluid in the stomach is rendered larger and more difficult of manipulation. Other things being equal, the amount of fluid secreted by the glands of the stomach is sufficient to render the digesting mixture sufficiently dilute. It is better for this reason not to drink fluids until after the solids at a meal have been swallowed, and perhaps better still to drink little immediately after a meal, but to take it four or five hours after one and before the next, so that the stomach may be practically washed out and made ready for the food of the next repast.

The necessarily brief survey of digestive processes set forth in the preceding pages leaves untouched much that is of great interest and value. The rapid advance in recent years in our knowledge of the physiological and chemical details of vital phenomena renders it difficult, almost impossible, in a small space to do justice to any subject connected with these sciences. Many of the observations which have lately thrown light upon the problems of digestion and nutrition are still uncorroborated, or are based upon so limited a number of experiments that it would savour of rashness to embody them among the generalisations treated of here. And again, many of the details of physiological chemistry are eminently technical and would serve only to confuse those who have no intimate acquaintance with this science, and who would have a difficulty in grasping the value to be attached to some small fact embedded in a matrix of chemical nomenclature. The subject of the digestion and absorption of food has received less attention than the importance of the subject merits. It may be that, as so commonly occurs, what we are constantly doing without a thought proves a matter of little interest.

Familiarity breeds contempt. This unthinking contempt is too often followed by sincere repentance when the digestive organs revolt against unlawful treatment.

Digestion plays an all-important part in the life-history of individuals and of species in every organism endowed with vitality; from the lowest members of the vegetable kingdom to the most highly developed and specialised animal, man, the struggle for existence centres upon the acquisition of food and the propagation of offspring, of which the first is indispensable for the second, the second for the continuance of the first. Plants flourish and multiply, furnish other plants and animals with food; these animals in turn may be devoured by others, only in time to die and return to the earth the nutriment originally removed by vegetable growths, whose seeds and saplings again remove it to furnish another generation of animals with food nourished upon the elements which supported their forerunners, and so the circle continues. Matter is indestructible. Living things are simply congeries of elemental atoms arranged to form tissues, and endowed with life. Remove the element of life and they resolve into these atoms, again capable of combining anew, it may be with very different comrades, to form other living tissues or some part, may be, of a rock. Elemental atoms undergo many more incarnations than were ever ascribed to Buddha. These ultimate atoms of matter *per se* have no connection with the inheritance of form or character. These must arise from a combination of atoms along with an inherited form of life. The combinations of atoms forming the seed require to be formed by their parent organism from certain elements. If these elements are only available in scanty amount, as when the parent is ill-nourished, diseased, or suffering from the effects of excess of physical work, of mental work, from excesses of any kind, some of the actual elements available for the formation of the germ may be withheld, apart altogether from the effect which all these conditions have upon the vital characteristics of the germs already fully formed. The greater the energy, health, and strength of the progenitors, either vegetable or animal, the greater will be the physical prowess of the offspring, and the more the food partaken by them approximates to the physiological ideal proper for their actions, processes, and environment, the more pronounced will be the vigour of their progeny, should the food

be employed with discretion. In these statements no allusion is made to the vexed question of the propagation of characteristics in virtue of any concrete quality of the vital force transmitted from parent to offspring by the germ. It is clear, however, that the nutrition of an embryo must influence most radically all the characteristics of its maturer growth. Agriculturists have long grasped this fact. The finest seeds yield the best crops, the animal in the best condition propagates the finest progeny. Man, however, is content to leave such matters to luck, and many of the puny, unhealthy children unhappily born into this world are practical and sad examples of the offspring of ill-fed, or over-fed, parents, who either cannot obtain sufficient food, or who indulge in the pleasures of the table to an unnatural extent. The nutrition of the parent affects not only the vital characters of the germ, but alters its elementary composition. Neuralgia has been said to be the cry of the nerves for more blood; rickets is an indication of an inability to use phosphates in the making of bone; ill-developed, faulty children are frequently due to a deficient supply of the substances needful to form normal abodes for the living germs *in utero;* ante-natal nutrition must profoundly influence the course of future life.

Observers have shown that variations in the food taken are capable of influencing the form and characteristics of the offspring of animals. Such variations are commonly brought about by gardeners in plants. By analogy there is every reason to suppose that the food taken by the higher animals influences their progeny in a similar manner, though not so markedly. Agriculture is based upon a knowledge, more or less empirical, of the nutritive powers of plants; they are regularly supplied with those substances which they stand most in need of, and which encourage their growth. Domestic animals are trained, fattened, their habits even are modified, to improve their stamina, to increase their fat, and to allow other foods to be relished. Man, partly owing to education of his senses, and partly to the changes produced by the introduction of money-values, is content or constrained in most instances to subsist on a diet much below that supplied to domestic animals in point of nutritional value and appropriateness; or if able to procure an unlimited amount of food, disregards his own rational rules for feeding his domestic animals, and indulges in all kinds of superfluous foods which only yield him the nitro-

gen and carbon requisite under the penalty of the disposition and expulsion of much useless, irritating, and often dangerous matter.[1]

Has the nutrition of mankind benefited by civilisation? Probably not. But the question is fraught with so many complex influences that no definite answer can be given. Possibly the selection of nutriment through the course of long ages has tended to develop some parts of the body to a greater extent than others. The brain tissue may have been rendered more capable of mental processes by the increased absorption of food suitable for its growth just as much as by hereditary transmission of mental characteristics. To be added to this, we must remember that this increase of brain nutrition is often accompanied by greater sensibility; the civilised man is constitutionally less able to bear pain and fatigue than the savage, although he may safely pass through trials, by reason of his increased power of inhibition, which would prove disastrous to the other. It is true that the civilised man of good antecedents, by training and healthy exercise, and by avoidance of mental strain during this period, may excel the untutored savage in feats of strength and of temporary endurance, but in doing so he imitates the savage's mode of life. Nevertheless, pit the one against the other in continuous effort and the savage will win, provided he has not tasted the sweets of civilisation. Probably no member of any savage tribe ever developed such physical prowess as, for instance, Sandow; but the ordinary savage, when able to procure sufficient food, is a very different being from the day-labourer or the office-clerk of civilised countries.

The finely-prepared dishes indispensable for the more leisured classes entail little trouble in mastication, taxing digestion by their bulk more than by their nature. The decay in the teeth of so many of the population may be largely put down to disuse. Foods are now so well prepared, even among many of

[1] Within recent times a discovery has been made by Schenck, of a character similar to many others which have previously been announced from time to time by zealous enthusiasts. The manner in which this "discovery" has been heralded is enough to raise suspicion about its value. No great discovery was ever be-puffed beforehand in this way, but it was found on subjection to analysis to be no mountain, but a very minute mouse. Schenck believes he can influence the sex of the offspring by dieting the mother, especially by giving her saccharine material for some time before and for a month or two after conception. The only people probably who will benefit will be the confectioners.

the labouring classes, that the teeth are not so necessary as of yore. In time, with the perfecting of our food preparation, teeth will be superfluous and man will become an edentulous animal. The old adage, "After breakfast walk a mile, after dinner rest a while," is only applicable to those who have to give all their powers to the digestion of their food. After breakfast the stomach is refreshed and strengthened by the period of quiet, and needs no help from its host; after dinner, the stomach, only recovering from a previous meal, may require a greater supply of blood to obtain enough digestive juice. Resting would supply this, allowing, by the disuse of other organs, more blood to flow to the alimentary canal. If the meal, however, be of food easily digested and absorbed, and consisting of much nitrogenous matter, work or exercise in moderation after it rather does good than harm by withdrawing blood from the stomach and helping to retard too great and too rapid an absorption of proteid bodies. This retardation is aimed at, according to Sir William Roberts, when tea, or coffee, or malt liquors are taken with food.

Shakespeare makes Petruchio say—

> "For 'tis the mind that makes the body rich;
> And as the sun breaks through the darkest clouds,
> So honour peereth in the meanest habit."

The mind, however, will not expand and enrich the body if impoverished from poor sustenance. Genius and poverty are seldom combined. A rustic or lowly genius is raised on honest food. Many of those credited with lofty powers, if brought up in poverty, have either inherited mental abilities and perspicuity whereby they are led early in life to properly nourish their brain and body, or belong to the class of eccentric geniuses whose powers are based on diseased mental conditions, and who soon exhaust their stores of energy, unable to continue an unequal and unnatural existence. The couplet in *Love's Labour's Lost*—

> "Fat paunches have lean pates; and dainty bits
> Make rich the ribs, but bankrupt quite the wits,"

illustrates the reverse side of the question. Over-indulgence in food is as ruinous to the brain as an inadequate supply. *Medio tutissimus ibis* is as true a maxim in the use of diet as in most other things.

A translation of the words written by Paulus Ægineta in the sixth century A.D. will fittingly close the discussion of the subject:—

"A lowering diet is safer than an excessive one for the preservation of health, but fails to impart tone and energy to the body from its lack of nourishment. A moderately nutritious diet should be taken by one suffering from the results of deficient nourishment. They who are wont to take exercise, and are able to rest when it pleases them, can do this with the least danger. . . . The articles of food which lie midway between the lowering and the stimulating are the best, and produce blood of a proper quality."

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